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# The Geographical Distribution of the Color-pattern Components of *Heliconius erato* and *Heliconius melpomene* with Genetical Evidence for the Systematic Relationship between the Two Species[1,2]

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(Plates I & II; Map 1; Text-figs. 1-15)

[This paper is a contribution from the William Beebe Tropical Research Station of the New York Zoological Society at Simla, Arima Valley, Trinidad, West Indies. The Station was founded in 1950 by the Zoological Society's Department of Tropical Research, under Dr. Beebe's direction. It comprises 250 acres in the middle of the Northern Range, which includes large stretches of government forest reserves. The altitude of the research area is 500 to 1,800 feet, with an annual rainfall of more than 100 inches.

[For further ecological details of meteorology and biotic zones see "Introduction to the Ecology of the Arima Valley, Trinidad, B.W.I." by William Beebe, Zoologica, 1952, Vol. 37, No. 13, pp. 157-184].

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## I. INTRODUCTION AND ACKNOWLEDGMENTS

THE most important early attempt to rationalize the diversity of color and pattern within the genus *Heliconius* was by Eltringham (1916), who based his conclusions upon macroscopic wing characters and an examination of the male genital valves. Recent genetical studies by Turner & Crane (1962) and Sheppard (1963) on material collected from Surinam and Trinidad, have shown that some of the more conspicuous components of the color-patterns of *Heliconius erato* and *Heliconius melpomene* are genetically linked and are capable of occurring polymorphically in both species.

Through funds supplied by the National Science Foundation, it was possible in 1963 to make field observations in two localities in Colombia and to observe and collect breeding material from several localities in eastern and western Ecuador.

The objectives of this project were, firstly, to test conspecificity within *H. erato* and *H. melpomene* by breeding; secondly, to confirm that similar color-pattern components occur sympatrically in both species so as to produce what appear to be mimetic pairs; and, thirdly, to observe the phenotypic characters of laboratory-bred heterozygotes and to obtain linkage data to test the closeness of the systematic relationship between the two species.

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ings and to Dr. E. W. Schmidt-Mumm[3] for considerable help and advice in Colombia. Dr. P. M. Sheppard, of the University of Liverpool, should be singled out for particular thanks as he has contributed a generous amount of his time to the evaluation of the conclusions to be drawn from the data and in statistically processing the data upon which the Text-figure histograms have been drawn.

## II. Materials and Methods

Three separate visits were made to Ecuador in 1963, from April 26 to May 15, from July 2 to 17, and from August 20 to 28. On the first trip the intention was to follow the system used on earlier trips to Surinam and collect eggs, larvae and pupae of local forms of *H. melpomene* and *H. erato* and return to Trinidad with the live immature material by a single-day jet flight from Guayaquil. However, great difficulty was experienced in keeping larvae alive during travelling in Ecuador because of mechanical and climatic disturbances, and because of the difficulty of providing a continuous supply of fresh food. All the larvae and pupae that were collected died, either in transit or later in Trinidad. Non-acceptance of Trinidadian *Passiflora* by larvae reared on exotic species also contributed to the extinction of the material. However, on the last day of the first trip, near Bucay, western Ecuador, a single male of *H. melpomene cytherus* and some females of *H. erato cyrbius* were caged in a box containing a pad soaked in a solution of sugar in water, and survived the journey back to Trinidad to form the foundation of the breeding stocks. These females which were already gravid, showed no hesitation in laying their eggs on the same species of *Passiflora* used by their Trinidadian counterparts and furthermore rejected any other species of *Passiflora* offered to them. While being brought back from the collecting locality by road, the box containing the adults was cooled by the intermittent application of external ice packs. On both subsequent visits, adults were caught in the field with a net, kept in cubical eighteen-inch gauze cages and fed on local flowers or a solution of honey in water. During long distance airplane flights the butterflies were transferred to small translucent paper envelopes and loosely packed in boxes with tissue paper. Using this method, mortality was less than 10%.

The normal mating and laboratory techniques have already been summarized by Turner & Crane (1962), but as an additional precaution against the particularly high incidence of virus disease, all the glassware was sterilized in an oven immediately before use and all food material and cotton wool pads were rinsed in a 5% solution of Milton, which is 1% sodium hypochlorite and 16% sodium chloride. Even so, mortality became so high that only by repeatedly changing the location of the laboratory rearing was complete extinction delayed, and ultimately the genetical experiments had to be abandoned. Mortality data are presented in the appendix.

The distributional data are based upon the examination of the collections of the British Museum (Nat. Hist.) at London and Tring, the Hope Department of Entomology at Oxford, the Paris Museum of Natural History and a portion of the collection of the American Museum of Natural History, as well as upon advice from Dr. E. W. Schmidt-Mumm on the Colombian fauna, and personal experiences in Ecuador and Colombia. Thanks are offered to the trustees and staff of the above institutions for study facilities.

## III. Description of the Wild Populations

The geographic and polymorphic variation in these two species is so diverse that to describe the distribution of the named forms unnecessarily complicates the task. Instead, the individual characters will be described and their distribution plotted on maps. By reference to the data in Table I, the characters may be related to the published names, of which those described prior to 1929 have been catalogued by Neustetter.

Confined to the neotropics, *melpomene* and *erato* probably occur in all areas where tropical or subtropical vegetation contains suitable species of the larval food plant *Passiflora,* and as far as can be ascertained the ranges of the two species grossly coincide (Map 1). The only localities where *erato* seems to occur on its own are in the valley of the Cauca river in Colombia, north of Nicaragua, along the east coast of Brazil and over its southern limits in Paraguay. *Melpomene*, as judged by museum data, is less common than *erato* in the south, and considering its habits of frequenting the more shady habitats it may have been overlooked at the southern extremity of its range, for even records of *erato* are very few beyond 25° South.

There is evidence that *melpomene* occurs in the absence of *erato* at about 1,250 meters in the eastern Ecuadorian Andes.

Within the latitudinal limits of their range, the principal regions where both species are absent are above 1,300 meters in the Andean, Guianian and Brazilian highlands, and west of the Andes south of Ecuador. It also seems unlikely that they colonize the tropical grasslands which comprise the llanos of Venezuela and the campos of Brazil. There are only sparse records from the area in southeastern Peru that is

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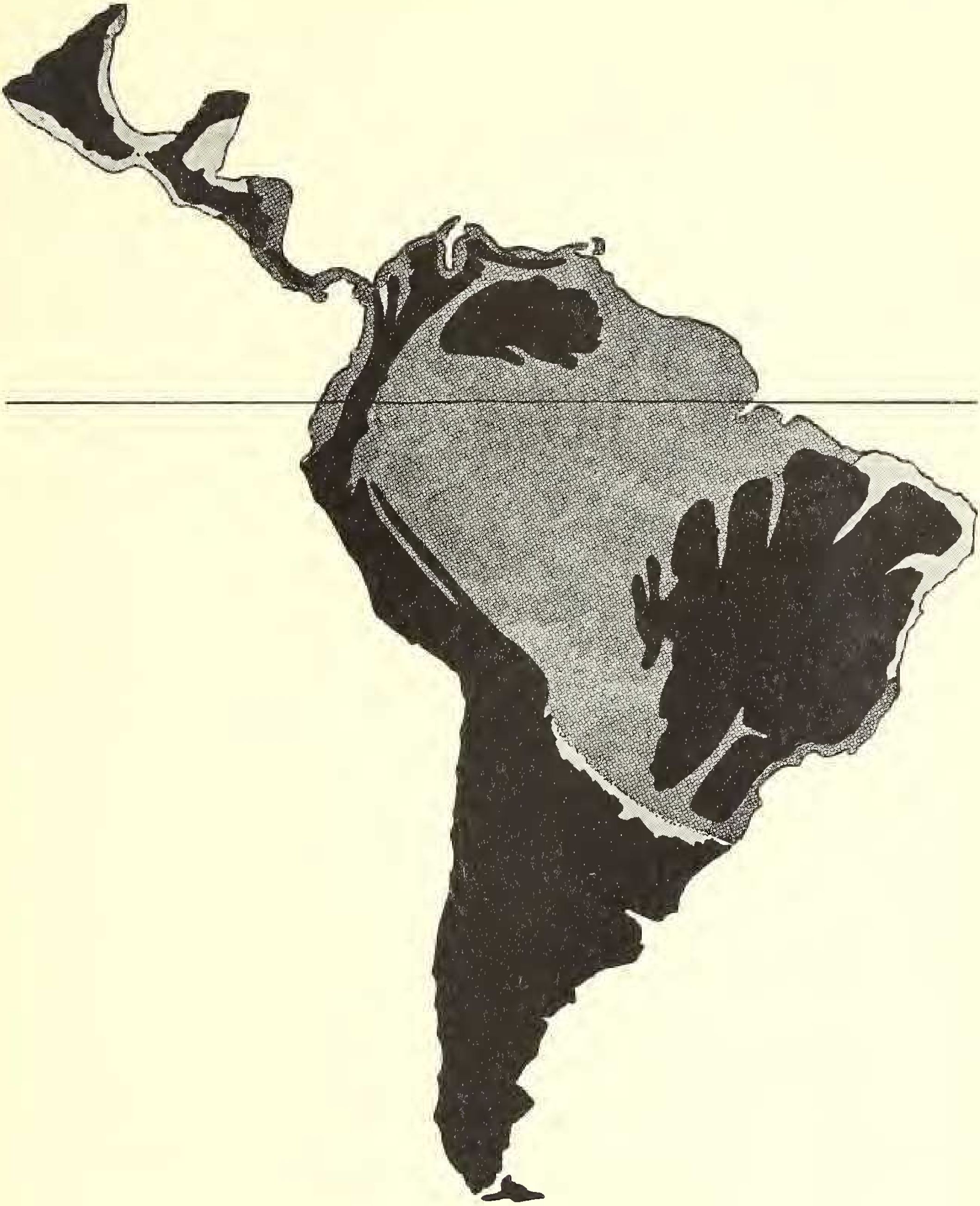
[3] Dr. E. W. Schmidt-Mumm, Optometra, Bogotá, Colombia.



Map 1. The geographical distribution of *Heliconius erato* and *Heliconius melpomene*. The black shaded areas are where neither species is known to occur, the darker shaded areas are where their distribution coincides, and the lighter shaded areas are where *erato* appears to occur on its own.

drained by the Madeira river, but this may be due only to inaccessibility, for it is flooded to a depth of a meter for at least two months of each year. Within their gross range it is likely that there are many areas where the ecological conditions are unsuitable, but our knowledge is focused around the commercial centers and waterways, for communications in South America are still very restricted. In the late nineteenth and early twentieth centuries, which is the period during which the bulk of the world's museum material was collected, communications were limited to river steamers, canoes and mule trains. Even now, motorized transport is at such a premium outside the cities of South America that sites for collecting are still influenced by availability as well as zoological reasoning.

Much of the early material is inadequately labelled. For example, "Ecuador" covers both sides of the Andes, and "west Ecuador" may still be a locality east of the Andes, for prior to 1942 Ecuador extended eastward as far as Brazil, and the eastern slopes of the Andes were still relatively "west." Ambarto and Quito are large towns lying between the crests of the twin mountain ranges, and such a locality label does not indicate whether the insect was taken on the western or eastern slopes, for both are far too high to be actual sites of collection. The same remarks apply also to Bogotá. "Amazonas" is a frequent label name, but not only is Amazonas-Brazil a vast area but there are "Amazonas" provinces in Venezuela, Ecuador and Bolivia as well. "Five days north of Cochabamba" is more useful, for in 1899 a journey was presumably accomplished either on foot or on mules. In some taxonomic groups data such as "eastern Ecuador" would be very useful, but in these species there are so many localized pockets of distinct forms that one needs to have such detailed information as "40 km. from Puyo on Puyo-Napo road, 800 m." Our earlier ideas on the prevalence of polymorphism have been exaggerated by the lack of precision in data from the eastern slopes of the Andes.

The color-patterns of both species are composed of a small number of similar components which are figured semi-diagrammatically on Plate I and described in detail below.

### *Heliconius erato* (Linnaeus 1758)

Ground-color (Pl. I, figs. 1-8). In all specimens studied, the ventral surface of both wings is a dull and uniform milk-chocolate brown (Pl. I, fig. 7), but the dorsal surface, though similar on both fore and hind wings, varies geographically from a brilliant structural blue iridescence (Pl. I, figs. 2 & 4), to a matt black (Pl. I, figs. 1, 3, 5). The most brilliant blue is exhibited by specimens from western Ecuador (*cyrbius* Godart 1819) and western Colombia (*venus* Staudinger 1882), whence there is a cline of decreasing blueness which forks in northern Colombia to Panama and Central America on the one hand and round the Guianian highlands into the Amazon basin on the other. Specimens from north of Costa Rica and south or west of Obidos are a matt non-iridescent black.

The iridescence of the northeastern continental forms is slight and somewhat ephemeral, for it is not visible in old or rubbed specimens. It might be possible to quantify the blueness by measuring the spacing of the striae, but this was beyond the capabilities of the equipment available. From the homogeneity of the iridescence on each wing it does seem that differences in blueness are due to differences in the structure of the individual scales rather than in the relative abundance of scales exhibiting iridescence. In all the specimens studied, the degree of blueness is greatest over the proximal half of both fore and hind wings and decreases distally, as in *Heliconius cydno, wallacei, sapho, sarae* and the other species that exhibit brilliant iridescence.

All the specimens known from the valley of the Cauca river in Colombia, that is between the western and central cordilleras, exhibit a bright iridescence which has a greenish hue unknown from other localities *(chestertoni* Hewitson 1872).

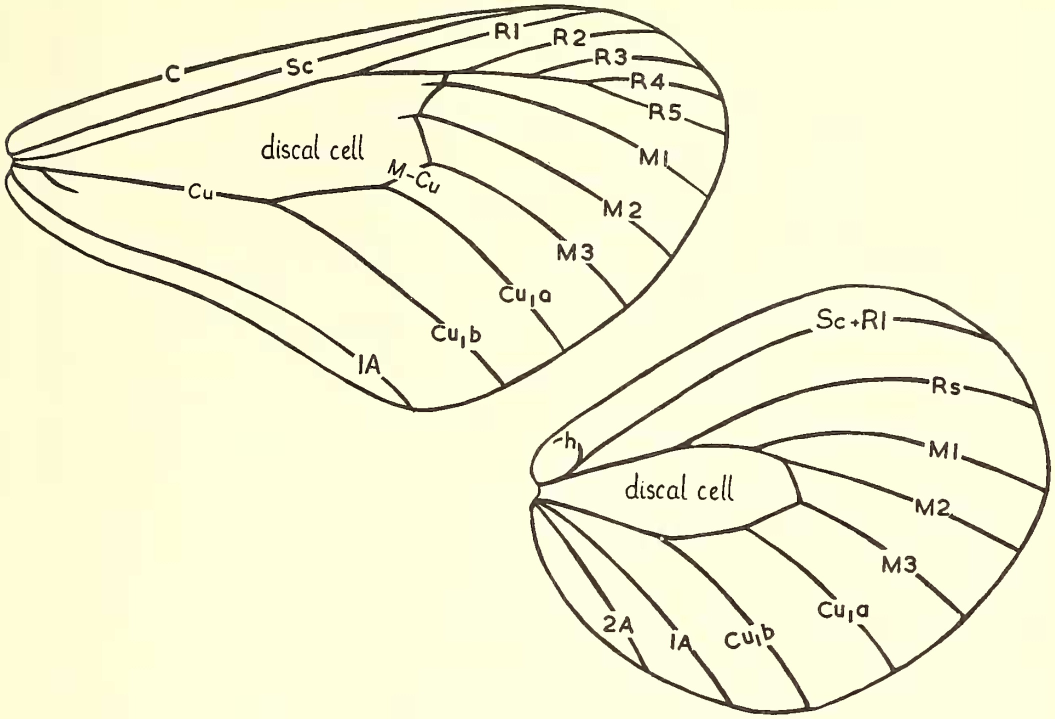
In northern Colombia, where the rate of change of blueness is greatest, there is considerable individual and local variation about a mean which is intermediate between the brilliant blue of the west coast and the dull blue of the northeastern continent.

In central British Guiana there are localities near the neighboring Essequibo and Demerara rivers where the iridescence is far in excess of the norm for that region *(magnificus* Riffarth 1900). The accuracy of the label data is confirmed by other characters.

Forewing Band (Pl. I, fig. 2; Pl. II, fig. 1; Text-figs. 1 & 2 A-N). The only localities where forewing band is known to be absent are as a rare polymorph in the Guianas *(oberthüri* Riffarth 1903), and as a monomorphic form in the valley of the Cauca river in Colombia *(chestertoni).*

In almost all cases the bands are grossly similar on both surfaces of the wing but the red bands are usually pale pink ventrally. As the coincidence of the bands on the two surfaces is not always exact, the descriptions and comparisions are based on dorsal characters only. Text-fig. 1 shows the conventional nomenclature of lepidopteran venation which will be used to facilitate description.

In Ecuador west of the Andes the red band is narrow along the length of the wing, and short across the width *(cyrbius,* Text-fig. 2A; Pl. I, fig. 2). There is only minor variation in band size, the narrowest of which was named *bellus* by Riffarth in 1907. Ecuadorian specimens are known *(diformatus* Riffarth 1900) in which the band is as broad as the narrower forms from western Colombia, but unfortunately the exact localities are unreliable.



TEXT-FIG. 1. Dorsal view of right fore and hindwings of *Heliconius,* illustrating venational nomenclature. **C**—costa; **Sc**—subcosta; **R1-R5**—first to fifth branch of radius; **Rs**—radial sector; **M1-M3**—first, second and third branches of the media; **Cu**—cubitus; **Cu1a** and **Cu1b**—branches of first cubitus; **1A** and **2A**—first and second anal veins; **H**—humeral branch of subcosta; **M-Cu**—medio-cubitus crossvein.

In Colombia west of the western cordilleras the band is very broad and long *(venus* Staudinger 1882, Text-fig. 2B), the increase in the width of the band taking place almost entirely in a distal direction, so the mid-point of the band is far beyond the apex of the discal cell. The boundary between *venus* and the narrow-banded *cyrbius* to the south is not revealed by the scanty locality records, and there is no obvious feature that could act as an obstruction to the free distribution of the two populations.

In the Cauca valley between the western and central cordilleras in Colombia, the only known form of *erato* is without a forewing band *(chestertoni),* but specimens are known from unspecified localities in Colombia in which there is a narrow short forewing band, like that of *cyrbius* or *bellus,* on the greenish-blue ground color known only in *chestertoni.* These specimens, named *molinus* by Grose Smith in 1898, may all be from the narrow northern open end of the Cauca valley where non-banded *chestertoni* would meet the medium-width long red-banded forms of northern Colombia. It will be shown later that the band of *cyrbius* and probably that from northern Colombia are under multifactorial control, so the intermediate character of the *molinus* band would be the expected result of such a hybrid. Other characters are also consistent with the intra-specific hybridic nature of *molinus.*

In northern Colombia, and in the Magdalena valley between the central and eastern cordilleras, the band is of similar length to that of western Colombia but is narrower and more symmetrically disposed about the apex of the discal cell *(colombinus* Staudinger 1896, *antigonus* Riffarth 1900, *guaricus* Reakirt 1868, Text-fig. 2C). Local variation is inconspicuous and is principally in the development of the emargination of the proximal boundary towards the junction of M-Cu and Cu 1 a. Intermediates between the western and northern Colombian bands are rare in museum collections and the only described form which has the anticipated appearance is *juno* Riffarth 1900 from Panama. The northern Colombian band also occurs in Panama, but beyond northern Panama the band becomes more frequently like the typically Mexican shape *(petiveranus* Doubleday 1847, *demophoon* Ménétriés 1857, Text fig. 2D), though intermediate bands like that of *tristis* Riffarth 1900 occur rarely as far north as Nicaragua.

East of the eastern cordilleras through the

Orinoco basin to the northeast of the Guianian highlands and into the Guianas, the band is red, long, broad and centered symmetrically over the apex of the discal cell (Text-fig. 2E). In the Guianas and along the lower Amazon to the southwest as far as Obidos, this band occurs polymorphically, but at low frequencies, with bands of other colors and shapes, but to the northeast it is monomorphic and it is quite typical in Trinidad. The name *hydarus* Hewitson 1867 has been applied to Trinidadian material, but not only is the band of the type-specimen of *hydarus* of atypical shape but there are a pair of unique red spots over the apices of the discal cells of the hindwings unknown in any specimens from Trinidad. Furthermore, the type locality of *hydarus* is Colombia, the majority of which is beyond the zone for which the Trinidad band-type is characteristic. Named forms with a band that is typical of the northeastern area of South America are *adanus* Seitz 1913, *vitellinus* Stichel 1919, both from Trinidad, and *dryope* Riffarth 1900, from the Guianas and lower Amazon.

The high degree of polymorphism in the Guianas is best understood after the monomorphic populations have been described.

Along the coastal strip of Brazil that borders the eastern side of the highlands, through Paraná, Rio Grande do sul, Paraguay and extreme northeastern Bolivia, the red forewing band is a characteristic crescentic shape with a distally bidentate margin *(phyllis* (Fabricius 1775*)*, Text-fig. 2F). The continuity of the red-banded forms from the polymorphism of the Guianas to the monomorphic *phyllis* zone is uncertain and is discussed later.

Along the eastern slopes of the Andes there are different forms of forewing band localized in valley systems and restricted to relatively narrow altitudinal limits. The dearth of accurate data from the Peruvian Andes makes the interpretation very unreliable, but the situation is probably very similar to that in eastern Ecuador where the author has personal experience.

The central region of South America, which is drained by the Amazon and its major tributaries, has exclusively yellow-banded forms of *erato,* but where these meet the red-banded forms, which have already been noticed in the Guianas, eastern Bolivia and east-central Colombia, there are polymorphic zones exhibiting red, yellow and red, and yellow bands. Hence, the large number of named forms. Along the Andes the upper altitudes have exclusively red or red and white banded forms, so the yellow bands of the central area are entirely surrounded by red, (Plate II, fig. 1).

The vague locality data on museum specimens from eastern Ecuador would lead one to believe it was an area of considerable polymorphism, but this is not the case. In Ecuador at Pastaza (Shell Mera) the only form present is *notabilis* Salvin & Godman 1868, which has a matt black ground color and a double band which is white with a narrow red peripheral border and with red in the posterior half of the proximal band (Text-fig. 2G). The amount of red varies considerably, as does the degree of separation of the two bands, for some examples are all white, others all red, but there is a tendency for the higher-altitude specimens to have the greater proportion of red on the bands, though in almost all specimens there is a variably small number of yellow scales intermingled with the peripheral red. One example was collected from a total of 52 from Pastaza in which the distal half of the outer band was missing, leaving the outer band as a narrow segment, a condition also known from museum collections and laboratory-reared specimens, and later referred to as "truncate."

Though *notabilis* seems to form the upper limit of the species in Ecuador at 1,150 meters, it descends to about 900 meters, at which level there are infrequent irregularities in the band shape with a tendency for them to fuse *(rosaceus* Riffarth 1907), and at 850 meters typical *notabilis* has been replaced by variable double white- and double yellow-banded forms, which may or may not carry dennis-ray patterns (see below). There was no opportunity to collect at altitudes between this and the 650 meter level, at which the band is monomorphically single and pure yellow, and there are few recognizably intermediate specimens in the museums visited (*ochraceus* Riffarth 1907). In the valleys of the Santiago river near Macas the outer band occurs in the total absence of the inner band (*etylus* Salvin 1871, Text-fig. 2M).

In the valleys of the upper tributaries of the River Huallaga, in northeastern Peru, there is a stable single-banded form, *favorinus* Hopffer 1874 (Text-fig. 2H) and *eratophilus* Joicey & Kaye 1917, the band shape of which is not unlike that from Trinidad, but it is yellowish-buff beneath. The only reason why forms intermediate between *favorinus* and the yellow-banded forms to the east are unknown seems the extreme inaccessibility of the area. In the valleys of the Chanchamayo and Perené rivers, which are tributaries in the complex system of the River Ucayali, there is a double-banded form (*microcleus* Kaye 1907, Text-fig. 2I), which is similar to *notabilis* but has much larger all-red bands. It probably occupies an ecological zone comparable to that occupied by *notabilis* in Ecuador.

Contrary to some data labels it is doubtful if *microcleus* ever exceeds 1,200 meters.

From a number of localities along the valleys of the terminal tributaries of the Beni and Madre de Dios rivers, like the Rivers Inambari and Songo, specimens of *erato* are known in which the red forewing band is a very broad long or short rectangle with a more or less prominent black crescent at the apex of the discal cell (*amphitrite* Riffarth 1901, Text-fig. 2J) and *unipunctatus* Joicey & Kaye 1917. As with *favorinus* the bands of specimens from the more upstream localities are yellow underneath.

The yellow-banded forms from the Amazon basin have two basic patterns from which all the remaining forms can be achieved by differential reduction and combination. The dominant pattern in the eastern continent is that of *H. erato erato* (Linnaeus 1758) (Text-fig. 2K) in which the band is divided across the apex of the discal cell and distally broken into spots. It is the major component of the polymorphic complex in the Guianas and lower Amazon, and may persist monomorphically in the coastal region to the east. The data on this point are unreliable, for the locality "Para" may mean anywhere in the province of Para and not necessarily near the city of Belem. Further doubt is cast on the yellow form reaching the coast monomorphically by the presence of yellow and red combinations to the southeast where red *phyllis* is definitely known from Marenham, together with combinations of *phyllis* and northern long red band. However, against this is the fact that no band form other than broken yellow is known from Belem or any locality between Bragance and the northern side of the Amazon estuary.

The principal sites of variation in this broken band are the posterior, anterior, proximal and distal quarters, each or combinations of which may be reduced to varying degrees. These variations may be combined with compaction of the spots and variation in the proportion of red to yellow, brought about by admixture of characters from other band forms. The extensive variation in the Guianas has led to a large number of named forms which really only define steps in a continuously varying population. The phenotypic characters of those forms represented in the British Museum, together with a few others whose descriptions are adequate, are classified in Table I.

As one proceeds westward along the Amazon the frequency of complete broken-band forms decreases, for there is regular increase in the degree and frequency of reduction of the proximal half of the band. By Teffé almost all specimens have only that part of the broken band that lies outside the discal cell represented, though some still retain a vestige in the antero-distal angle (*lativittus* Butler 1877, *divus* Stichel 1906). Above the contour passing through Iquitos the band is completely outside the discal cell and is of shorter but more variable length (*estrellus* Bates 1862, *emmus* Riffarth 1901, Text-fig. 2L). As mentioned above, undoubted intermediates between the *emmus* band and the double *notabilis* band of higher altitudes are uncommon.

The second elemental yellow band shape from the Amazon basin is more compact, short in length and centered over the apex of the discal cell. The typical form, *venustus* Salvin 1871 (Text-fig. 2N), is characteristic of the valleys of the tributaries of the River Madeira in west-central Brazil but this "compact" band invades the northern area dominated by "broken" band, and intermediates such as *udalricus* (Cramer 1780) from the Guianas and the lower and middle Amazon may be due to the combination of "broken" and "compact" band characters.

In the Guianas the variety is even more complex because of the addition of long broad band from the north and perhaps some characters unknown elsewhere. The super-broad band of *magnificus* from British Guiana, which is superficially like that of *amphitrite* (Text-fig. 2J), is relatively constant and seems associated with the more brilliant iridescence than that of neighboring forms, through there is no genetical evidence for linkage.

In the shallow valleys of the rivers Mamoré, Guaporé and Rio Grande, which drain central Bolivia, the red-banded forms from the eastern Andes and Paraguay meet the compact yellow bands of the lowlands. The result is a polymorphism which approaches that of the Guianas in its complexity. The combinations of *venustus* yellow-compact band, southern *phyllis* crescentic-red band and the super-broad-red band of *amphitrite* produce a host of intermediates, the named forms of which are phenotypically classified in Table I.

The only other locality where the absence of an altitudinal barrier allows the central region yellow-banded forms to meet peripheral red-banded forms over a broad area is in south-central Colombia between the eastern cordilleras and the llanos of Venezuela, though there seems also to be a leak through the southern end of the Magdalena valley. The number of specimens from this area is small, presumably because of inaccessibility, but they all show combinations of characters as in the Guianas and Bolivia. They have been included in the phenotypic classification in Table I.

Forewing Fleck. The yellow or white patches that may occur proximally on the forewing band of *melpomene* in western Ecuador are unknown in *erato.*

Dennis (Pl. I, fig. 1; Pl. II, fig. 2). The name "dennis" was given by Turner & Crane (1962) to the element of pattern in which the approximate basal third of the forewing is red (Pl. I, fig. 1). The amount of red is variable, particularly in the Guianas, but except in southwestern Brazil it is prominent on both wing surfaces, though in no case does it extend over the posterior part of the forewing that normally covers the anterior part of the hindwing. Together with the red forewing base there may be a trace of red at the extreme base of the hind wing, but not so as to form a longitudinal bar as in *melpomene* (Pl. I, fig. 3). The geographical area over which dennis occurs monomorphically extends westward from Obidos to the slopes of the Andes at an altitude in Ecuador of about 850 meters, and southward around the plateau of Matto Grosso to Bolivia and Peru up to an altitude of about 300 meters (Pl. II, fig. 2). To the northeast of Obidos dennis and non-dennis occur in the same polymorphic population as far as British Guiana, but beyond that dennis is unrecorded. A similar polymorphism is found in central Bolivia, along a narrow altitudinal zone in the eastern Andes and in southern Colombia where dennis again makes an interface with non-dennis. In specimens exhibiting dennis and double band, dennis is separated from the proximal boundary of the inner band by a narrow line of ground color (as in Pl. I, fig. 1), but when it occurs with single band it may be a little more extensive distally and less precisely defined. The presence or absence of dennis has greatly multiplied the number of named forms, and these are included in Table I.

Ray (Pl. I, fig. 5; Pl. II, fig. 2). Usually occurring with dennis, but rarely on its own *(anaitis* Riffarth 1907), ray (Turner & Crane, 1962) is a series of radiating lines emanating from a red discal bar on the upper and lower surfaces of the hind wing (Pl. I, fig. 5), though most frequently the upper surface rays are more prominent. Ray is composed essentially of a red center to the discal cell and red lines in the open cells behind each of the radiating veins Sc+R1, Rs, M1, M2, M3, Cula, Culb, 1A and 2A, but the rays behind Sc+R1, and Rs are not expressed in males, as androconia are borne on the dorsal surface of that area. The red on the discal cell, and/or that behind Culb, may divide to reveal a central streak of ground color. The width and intensity of the rays in the middle and lower Amazon is greater than elsewhere *(amazonus* Staudinger 1896 and other forms) though there is variation in all localities. The gross distribution of ray coincides exactly with that of dennis (Pl. II, fig. 2), but whereas the occurrence of dennis without ray is common in the Guianas, it is much less common in the other polymorphic zones. These combinations have contributed to the large number of named forms tabulated in Table I.

Hindwing Yellow Bars (Pl. I, figs. 4 and 7; Pl. II, fig. 2). In western Ecuador and western Colombia there is a longitudinal yellow bar centered over the posterior margin of the discal cell on the ventral surface of the hindwing (Pl. I, fig. 7). The heterozygous condition of this bar is a similarly located but barely perceptible differentiation of the brown ground color (see genetics section), and is known in the wild from the Cauca valley (*nocturnus* Riffarth 1900), from Panama (*juno* and *tristis*), northern (and rarely eastern) Colombia (*guaricus*) and Bolivia (*clelius* Neustetter 1927, *phyllidis* Grose Smith 1892). However, the true distribution of ventral yellow bar is masked, for dorsal yellow bar, which is a coincident yellow bar on the dorsal surface (Pl. I, fig. 4), seems also to express itself ventrally. No instances are known of dorsal bar in the absence of ventral bar. Dorsal bar extends monomorphically from northern Panama to Mexico, (*demophoon* and *petiveranus*), along the Cauca valley in northern Colombia (*chestertoni*), along the upper tributaries of the Hualaga river in northern Peru (*favorinus*) and around the coastal strip of Brazil, through Paraguay to eastern Bolivia *(phyllis).* The bar occurs polymorphically in the Magdalena valley, northern Colombia and Panama, and with a high incidence of apparent heterozygosity in east-central Bolivia. These localities are all areas on the interface between bar and non-bar forms. The nature of the heterozygotic expression of dorsal bar is without experimental evidence, but in Bolivia, where the variation is most diverse, the phenotypic expression of bar may take one of the following four forms: a complete dense bar on both surfaces, sparsely scattered yellow scales on both bar surfaces, restricted dense portions of bar on both surfaces, and localized dense portions of bar on the dorsal surface only. It will be shown in the next section that ventral bar is controlled by a single pair of allelomorphs but as it is possible that there is interaction between the expression of dorsal and ventral yellow bar, and there may be more than one controlling gene for dorsal yellow bar, further analysis has not been attempted. Additional evidence is available in the combinations of bar with ray in Bolivia. There, bar may overprint the rays, be overprinted by the rays, be under the rays but overprint the normally black veins, or be masked by both rays and veins. It should be noted that whereas the evidence from Bolivia suggests that the heterozygous condition of dorsal bar should be recognizable, very few specimens with an intermediate condition between dorsal bar and non-bar are known from northern Colombia and Panama. The few possibles that are known (e.g., *nocturnus*) show a very sparse scattering of yellow scales over the dorsal bar position, which is a condition that has appeared in the laboratory $F_2$ progeny of *cyrbius* and *adanus* crosses. As *cyrbius* has only ventral yellow bar, even this character may not be attributable with certainty to dorsal yellow bar.

There is considerable regional variation in the shape of bars. In western Ecuador the ventral bar of *cyrbius* is variable in intensity, but always long, narrow and with a vague periphery. In western Colombia the ventral bar of *venus* is about twice as wide as that of *cyrbius* and uniformly dense yellow with a precise boundary. The dorsal and ventral bar of northern Colombia, Panama and Costa Rica is shorter but broader with a ragged periphery, whereas from Guatemala to Mexico it is similar to the narrow bar of western Ecuador but uniformly intense and with a precise boundary. The change-over takes place about Nicaragua, as does the change in iridescence and band shape, though in the transitional localities both types of bar and intermediates may be found. The bar of the Huallaga river system has a very precise boundary but is otherwise similar to the short broad bar of northern Colombia; there is also a similar absence of recognizable heterozygotes, but this may be due to the inaccessability of the locality and the relatively small number of specimens known. In central Bolivia and south Brazil the narrow long bar again has the margins more precisely defined and with a smoother surface texture like that from Central America north of Costa Rica. Though the regional differences in bar shape and texture could be due to geographically distinct modifying genes, the apparent difference in the heterozygous behavior suggests that more than one major gene is involved. There are as yet no experimental data available.

HINDWING WHITE MARGIN AND FRINGE (Pl. I, fig. 4). In western Ecuador the terminal scales at the periphery of both fore and hindwings of *cyrbius* are totally white, and on both the upper and lower surfaces of the hindwing the white invades the membrane from a pair of centers between the terminations of each pair of veins. The proximal boundary of the paired white hindwing patches are asymmetrically convex. Within the Ecuadorian populations there is little variation but near the boundary with *venus* in Colombia the width and density of the margin is variable. There may be some yellow scales intermingled with the white, but the yellowing always proceeds from the proximal margin.

In western Colombia north of a line approximating to the River Patia the white margin is reduced abruptly to a complete fringe of white scales with no encroachment onto the membrane *(venus)*.

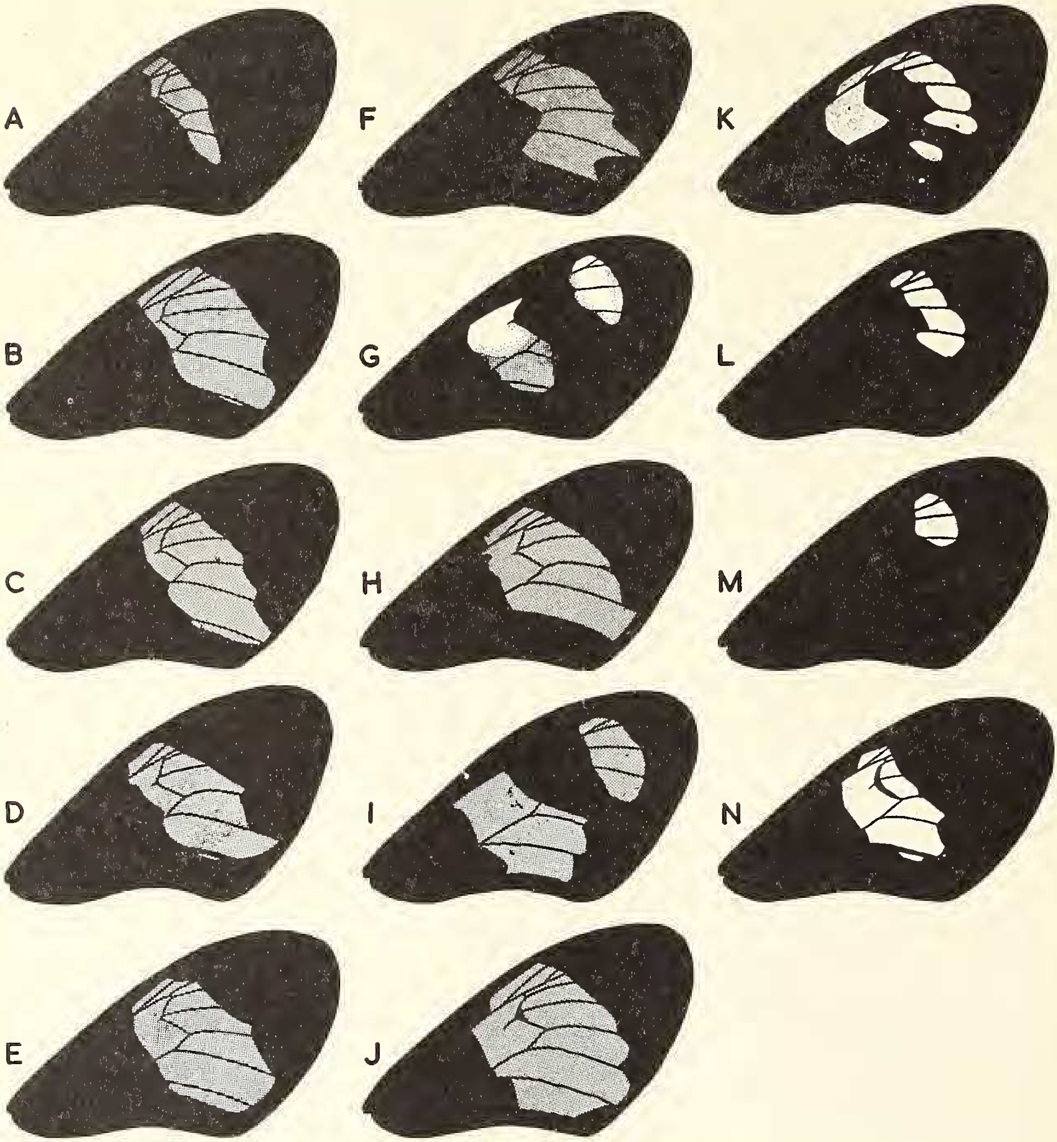
In the Cauca valley and elsewhere over the whole range of *erato* there are no white scales on the margin of either fore or hindwing, except for the rare occurrence in west-central Bolivia of forms in which there are a pair of small submarginal intervenal white spots on the posterior border of the hindwing, and associated with which are double radiating lines of white scales as in *Heliconius wallacei, doris, aoede, xanthocles* and several other species.

FOREWING YELLOW LINE (Pl. I, figs. 1 and 2). This character is a narrow yellow line on both surfaces of the forewing which lies slightly obliquely over Cu1 and which terminates just distal to the fork of Cu1 into Cu1a and Cu1b. In *erato* it occurs only in coastal and southern Brazil, Paraguay and eastern Bolivia (*phyllis*), but it is also a feature of *Heliconius wallacei, sarae, antiochus, doris* and several other species.

The yellow spot at the dorsal base of the forewing, which occurs as a rarity in the Guianas but becomes very frequent among Amazonian populations, is coincident with the proximal origin of the forewing line. In the line/non-line zone of eastern Bolivia there is considerable polymorphism as well as variation in the intensity of expression of line.

FOREWING COSTAL SPOT. This is a small rectangle of red at the ventral base of the forewing, lying between the costal and subcostal veins. It is a feature of *erato* everywhere except in the Cauca valley where it is absent, though in western Ecuador and at the higher levels in the eastern Ecuadorian and Peruvian Andes it is variable. In 160 museum specimens from the Quevado district of western Ecuador, 96 were without any evidence of a costal spot and in the remainder there was considerable variation in its size. In forms exhibiting dennis the costal spot is usually masked, though it may sometimes be detected as a more intense red.

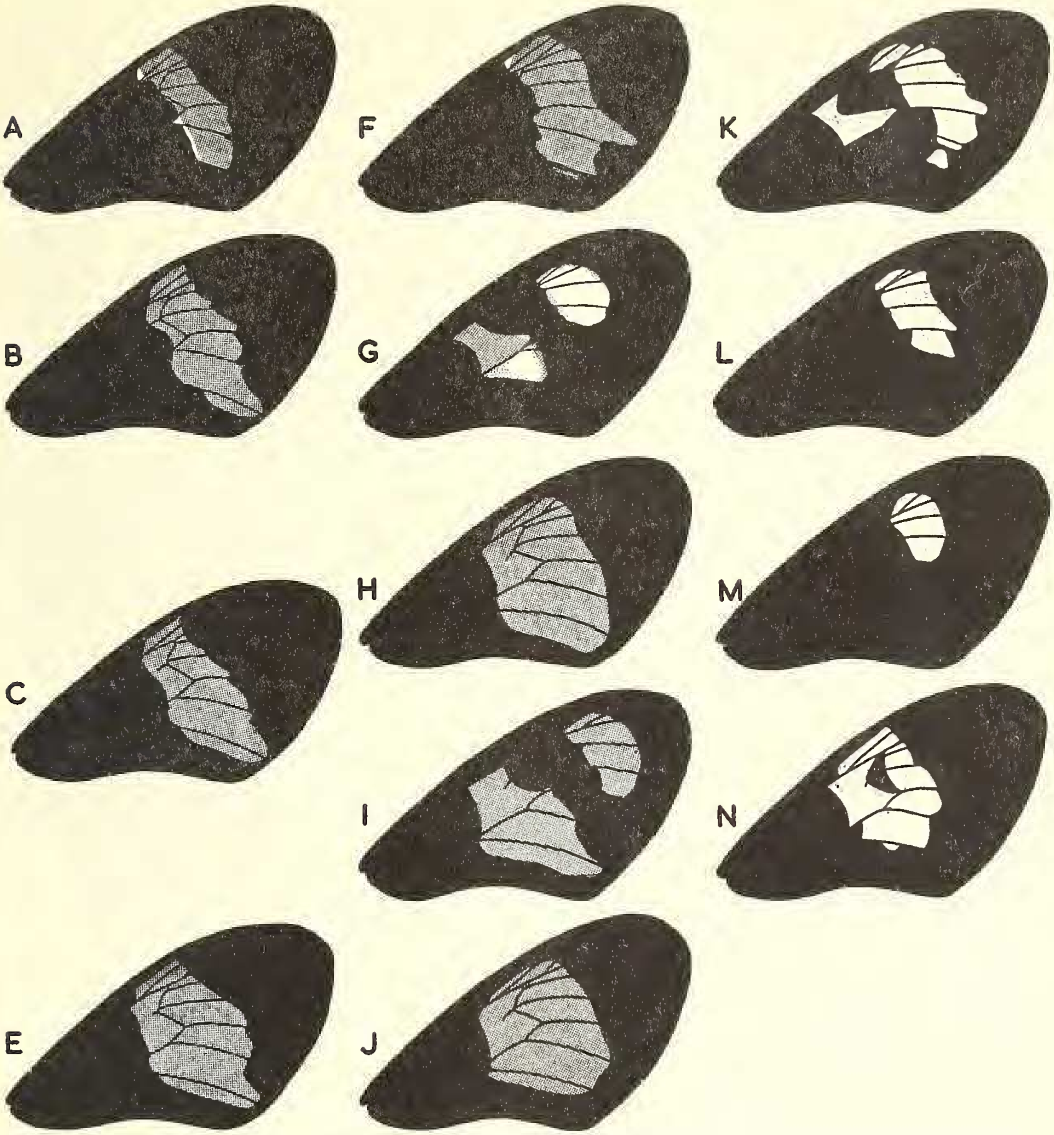
HINDWING COSTAL STREAK (Pl. I, fig. 7) is a yellow border along the leading edge of the ventral surface of the hindwing, which is most broad inside the recurrent branch of the subcostal vein and which tapers off midway along the length of the wing. In forms exhibiting ray, the yellow



TEXT-FIG. 2. Right dorsal forewing bands of *Heliconius erato*. The shaded areas on figures A-J are red and those of K-N are yellow. **A**—*cyrbius*, western Ecuador; **B**—*venus*, western Colombia; **C**—*colombinus*, northern Colombia; **D**—*petiveranus*, northern Central America; **E**—*adanus*, northeastern South America and Trinidad; **F**—*phyllis*, eastern and southern Brazil; **G**—*notabilis*, 800-1,100 meters in eastern Ecuador; **H**—*favorinus*, upper River Huallaga, northeast Peru; **I**—*microcleus*, upper River Ucayali, central-eastern Peru; **J**—*amphitrite*, upper Beni and Madre de Dios rivers, southeastern Peru; **K**—*erato*, the broken band of the Guianas and middle and lower-middle Amazons; **L**—*emmus*, upper and middle-upper western Amazons; **M**—*etylus*, upper Santiago river system in southeastern Ecuador; **N**—*venustus*, the compact band of southern middle Amazons. All approximately 1½ times natural size.

may be reduced to a few basal scales, but some yellow can always be identified. Though locally variable in extent, the only locality from which the yellow costal streak is absent is in the Cauca valley (*chestertoni*).

HINDWING BASAL SPOTS (Pl. I, fig. 7). These are a cluster of up to four red spots at the ventral base of the hindwing. In western Ecuador they are very small though distinct, but in western Colombia the number varies from none to four. In the Cauca valley *chestertoni* may have none or one, and the intermediate *molinus* two to four. Elsewhere four is the rule, and even where they are masked by ray, their presence can usually



TEXT-FIG. 3. Right dorsal forewing bands of *Heliconius melpomene*. The shaded areas on figures A-C and E-J are red and those of K-N are yellow. A—*cytherus*, western Ecuador; B—*vulcanus*, western Colombia; C—*rosinus*, northern Colombia and Central America; E—*flagrans*, northeastern South America and Trinidad; F—*besckei*, southeastern Brazil; G—*plesseni*, 800-1,100 meters in eastern Ecuador; H—*amaryllis*, upper River Huallaga, northeast Peru; I—*xenocleus*, upper River Ucayali, central-eastern Peru; J—*euryades*, upper Beni and Madre de Dios rivers, southeastern Peru; K—*thelxiope*, the broken band of the Guianas and middle and lower-middle Amazons; L—*elevatus*, upper and middle-upper western Amazons; M—*ecuadorensis*, upper Santiago river system in southeastern Ecuador; N—*vicinus*, the compact band of southern middle Amazons. All approximately 1½ times natural size.

be detected by the more intense red at the spot locations.

HINDWING APICAL CREAM RECTANGLES (Pl. I, fig. 7). Specimens from south and southeastern Brazil typically have two or three cream rectangles set subapically at a tangent to the periphery of the ventral surface of the hindwing, just beyond the distal extremity of the ventral yellow bar. In central Bolivia this character becomes variable in presence as the population merges with the Amazonian one in which this character is absent. Specimens have been seen in which the site of the rectangles is perceptible as a slight differentiation of the ground color; this may be the heterozygous condition.

Hindwing Ventral Red Raylets (Pl. I, fig. 7). Specimens from south and southeastern Brazil may have a line of three to six red triangular raylets posterior to the ventral yellow bar, one between each of the hindwing veins (*artifex*). The proximal pair may be double.

Body Color. Though the body is mainly black, there are light markings on the head, thorax and abdomen, which are predominantly yellow everywhere except in specimens from western Ecuador, western Colombia and the Cauca valley, in which cases they are white. Outside these localities the yellow head markings bear a variable quantity of white scales which are most abundant on the lateral occiput, the frons and the antennal bases. The partial yellow color of the palps serves to distinguish *erato*, and usually *melpomene*, from the very similar sympatric species *aoede*, *xanthocles*, *egerius* and *burneyi*, in all of which the palps are pure white.

### *Heliconius melpomene* (Linnaeus 1702)

Ground Color (Pl. I, figs. 1, 3, 6 and 8). The situation is similar to that pertaining in *erato* except that in *melpomene* the blue iridescence is always a little less intense than that of sympatric forms of *erato*. No super-brilliant specimens like the Guianese *erato magnificus* are known.

Forewing Band (Pl. II, fig. 1; Text-figs. 3A–N). In western Ecuador the band of *cytherus* Hewitson 1869 is similar in color, shape, location and relative size to that of the sympatric *cyrbius* (cf. Text-fig. 2A & 3A), the only conspicuous feature distinguishing the *melpomene* band being the whitening of the proximal margin which is here termed "forewing fleck."

In western Colombia the band of *vulcanus* Butler 1865 is broad and long and only just fails to meet the posterior margin of the wing (Text-fig. 3B). Distally there is emargination of the band along the veins, particularly along Cu1a, so the band is slightly narrower than that of the sympatric *venus* and more symmetrically disposed about the apex of the discal cell. There are insufficient localities to determine the geographical boundary with *cytherus*.

In northern Colombia, excluding the Cauca valley where *melpomene* is unknown, and northward into Central America, the forewing band of *rosinus* Boisduval 1870 and *euryas* Bates 1862 is of medium width but long and similar to the sympatric forms of *erato* (cf. Text-figs. 2C & 3C). Unlike *erato* there is no differentiation of a characteristic northern Central American band shape, for *melpomene* is not known to occur north of Nicaragua.

To the east of the eastern cordilleras in Colombia, the band of *melpomene* (Linnaeus 1702) and *flagrans* Stichel 1919 is long, broad and red but though similar in shape and distribution to that of the sympatric *erato* (cf. Text-figs. 2E and 3E), it is much less common in the polymorphic complex of the Guianas and lower Amazon. It is again most convenient to leave the consideration of the polymorphic areas until last.

The southern forms comparable in appearance and distribution with *erato phyllis* are *besckei* Ménétriés 1857 and *nannus* Stichel 1899 (cf. Text-figs. 2F & 3F). Though no *melpomene* are known from the east coast of Brazil, even *erato* records are very few and it is possible that *melpomene* has been overlooked. One would expect to find the *besckei* band in this area.

The zonation in eastern Ecuador parallels that of *erato* exactly, with *plesseni* Riffarth 1907 flying in the *notabilis* zone (cf. Text-figs. 2G & 3G), and with many varieties occurring along the interface between the stratum containing the double red and white band non dennis-ray form and that containing the single yellow band dennis-ray form; some of those named are included in Table I.

In the terminal valleys of the Huallaga river system the forewing band of *amaryllis* Felder 1862 is long, broad, single and red and is rather similar to that from the northeastern part of the continent, but it also approximates quite closely to that of the sympatric *erato favorinus* (cf. Text-figs. 2H & 3H). Specimens are known from Chazuta (300 meters) in which there are proximal yellow scales on the red band, so this is probably near the downstream boundary with the all-yellow band forms. *Amaryllis* extends along the Huallaga river at least as far as Tingo Maria (750 meters), where it almost unites with *xenocleus*.

*Xenocleus* Hewitson 1852 is the characteristic double red-banded form of the upper Perené river where it coincides with the very similar *erato microcleus* (cf. Text-figs. 2I & 3I).

The large red band of *erato amphitrite* in the upper Madre de Dios river is matched by that of the sympatric *euryades* Riffarth 1900 (cf. Text-figs. 2J & 3J).

As in *erato*, the Amazon basin is occupied by yellow-banded forms, but though the total effect is similar, their constitution is more complex. One of the basic patterns in the middle Amazon is a "broken" band typified by *thelxiope* (Hübner 1806) (Text-fig. 3K) and, as in *erato*, there is reduction of the proximal and posterior portions of the band as one travels in a westward direction. This trend produces such forms as *agalope* Felder 1862 and *elevatus* Nöldner 1901 (Text-fig. 3L) before reaching the very reduced band of *ecuadorensis* Neustetter 1908 (Text-fig. 3M). This oval band occurs in the valley of the upper Napo at Archidona as well as in the upper Santiago river district, but it seems unlikely that the *ecuadorensis* band is homologous with that of *erato etylus,* for its more proximal location suggests that it is a remnant of the antero-distal portion of the broken band rather than a distinct character. The comparable band in *erato etylus* is of more restricted geographical distribution and is probably homologous with the outer band of the double-banded *notabilis.*

There is a compact band type exemplified by *vicinus* Ménétriés 1875 (Text-fig. 3N) which is most frequent in the southwestern Amazons, but which does invade the lower and middle Amazon area at lower frequency, as in *erato.*

The extreme complexity of band in *melpomene* is principally due to the occurrence, at high frequency in the Guianas and at decreasing frequency to the south and west, of what is here called the Z-band (not figured because of its variability). Sheppard (1963) founded it in his material, and in his breeding program the homozygous condition appeared as a broken yellow band with a distal narrow long band of red. The heterozygous condition, in combination with Trinidad long broad red band (*adanus*), had the yellow reduced proximally, but it seems that there may be a series of allelomorphs at this locus, so more breeding data are required. The distinguishing feature of the band is the sharp interface between the red and yellow which lies along a transverse line which is deflected proximally in cell Cu1a through about fifty degrees. A similar interface also occurs in *melpomene heurippus,* which is not considered a distinct species, and in the wild hybrids *rubellius, wernickei* and *emilius.* The red spot at the posterior forewing margin of *timaretus* and its polymorphs is the posterior vestige of this band. In the intraspecific hybridization zone of central Bolivia the red and yellow band combinations only rarely have the Z-band type of interface, it being much more common for the red and yellow scales to intermingle over a broad area; in these individuals the Z-band character is considered to be absent.

In Para, the Z-band character, with broken yellow band, extends as far as Bragance on the coast so it is unlikely that the population of either *melpomene* or *erato* is strictly monomorphic in this area.

The taxonomic status of *tumatumari* Kaye 1906 and *bari* Oberthür 1902 has not been confirmed, but if they are *melpomene,* as seems most likely, they are the only forms in which there is a subapical band beyond the principal broken yellow band. This is a character of wide occurrence in other species.

FOREWING FLECK (Text-fig. 3A). In western Ecuador there may be up to three white or partly yellow flecks associated with the proximal margin of the forewing band. It is probably better to regard these flecks as lightening of the band rather than as discreet items. The flecks comprise a conspicuous light rectangle over the origin of R1, a less conspicuous triangle in the angle between the M-Cu cross-vein and Cu1a, and a vague area which may be reduced to a few light scales along the posterior proximal margin of the band. The expression of the white is variable and any of the flecks may be reduced to a few scales, or they may coalesce and form an irregular transverse white strip along the proximal border of the band. This variation in the extent and color of the flecks has given rise to the naming of several forms. North of the River Patia, in western Colombia, fleck is less common than in Ecuador, in northern Colombia it is a rarity, and elsewhere the only locality in which light fleck is known is southeastern Brazil where the yellow spot over the origin of R1 is a constant feature of *besckei.*

DENNIS (Pl. I, figs. 1 and 3; Pl. II, fig. 2). Though dennis on the forewing is similar in *melpomene* and *erato,* the considerable difference between the two on the hindwing is illustrated on Pl. I, figs. 3 & 4, where it is shown that in *erato* dennis has little or no expression on the hindwing whereas in *melpomene* there is a narrow red longitudinal bar which is always expressed in combination with the red base to the forewing. The dennis markings appear on both surfaces of the wing, though in southwestern Brazil the expression of dennis on the ventral surface is weak, and they may occur with or without ray (see below). The geographical distribution will be discussed under ray, for most commonly these characters are associated together.

The narrow posteriorly concave bar of dennis is frequently enlarged by the addition of a biconvex red bar which in shape is not unlike the yellow dorsal bar discussed below. The presence or absence of the biconvex bar accounts for the discontinuous variation in the breadth of the gap between the bar and the anterior margin of the rays when they are present. The only example known in which the broad red bar occurs in the absence of dennis is *amandoides* Neustetter 1926, though in *margaritus* Riffarth 1900 the yellow dorsal bar has red scales intermingled. Both are from Bolivia.

RAY (Pl. I, fig. 6; Pl. II, fig. 2). Ray in *erato* and *melpomene* differs in appearance, for whereas *erato* has the rays radiating from a red center to the discal cell, in *melpomene* the rays emanate from the bar of dennis if present, or if not, then from the position where it would be. The rays in eastern Ecuador and Peru may be proximally thickened so they resemble nails with large heads; the former is the only locality in which rays are known to occur in the absence of dennis (*virgatus* Stichel 1902). Though the inheritance of dennis and ray is distinct, ray on its own is not yet recorded from the Guianas. The distribution of dennis and ray is similar and extends as shown in Pl. II, fig. 2, over the whole of the Amazon basin. Of special interest is the limitation of dennis and ray to below 850 meters in the eastern Ecuadorian Andes, which is the altitude at which yellow band is also limited. Red forewing band and dennis-ray combine only in the peripheral polymorphic populations. The only exception to the restriction of yellow band and dennis-ray to 850 meters is the occurrence of *timaretus* above 1,250 meters in the Pastaza valley, where it occurs beyond the range of *erato*. As discussed later it is considered a relic.

HINDWING YELLOW BARS (Pl. I, fig. 8; Pl. II, fig. 2). The geographical distribution of the dorsal and ventral yellow bars in *melpomene* is comparable with that in *erato*, but the appearance of the bars differs in detail. In western Ecuador (*cytherus*), western Colombia (*vulcanus*), northern Colombia and Central America (*rosinus*), the bars are far less varied than in *erato* and are of medium width with the edges of the bars clearly defined in all localities except western Ecuador.

Just as in *erato*, the heterozygous ventral yellow bar is a faint differentiation of the ground color which is known in the wild only from the Magdalena valley, northern Colombia, Panama (*euryas*) and Bolivia. No obvious heterozygous condition of the dorsal yellow bar is known, nor is the dorsal bar known to occur in the absence of the ventral bar.

Both bars are present with a crisp boundary in *amaryllis* which coincides exactly with *erato favorinus* in the valleys of the tributaries of the Huallaga river. The bar/non-bar boundary seems to approximate to Balsapuerto (225 meters), which is near Yurimaguas in northeastern Peru.

The yellow bars of *besckei* and *nannus* coincide with those of *erato phyllis* in southern and southeastern Brazil, and in central Bolivia there is a similar degree of polymorphism at the interface with non-bar forms. Though the heterozygous (?) behavior of the bars in this polymorphic zone is directly comparable with that of *erato*, the shape of the bars is more variable, there being a particularly common form in which the bar is parallel-sided and almost rectangular (Plate I, fig. 8).

FOREWING YELLOW LINE (Pl. I, fig. 1). Though similar both in appearance and distribution to that of *erato*, it occurs also in western Ecuador (*cytherus*), where it is prominent only on the ventral surface.

FOREWING COSTAL SPOT. Morphologically similar to that of *erato*, it is also a constant feature over the whole range of *melpomene* except in western Ecuador, western Colombia and the valley of the Huallaga river, where it is of variable occurrence.

HINDWING COSTAL STREAK (Pl. I, fig. 8). Similar to that of *erato*, it is present everywhere, though when in association with ray it may be reduced to a yellow spot enclosed by the recurrent humeral branch of the subcosta. It seems somewhat variable in presence in eastern Ecuador at about 900 meters, and may be red (*ecuadorensis*) or red and yellow (*aurofasciatus* Neustetter 1928).

HINDWING BASAL SPOTS (Pl. I, fig. 8). Though similar in location to those of *erato*, the maximum number of round spots is three, for the red mark between Rs and Cu is either a small triangular fleck or absent. In western Ecuador (*cytherus*) and western Colombia (*vulcanus*) the spots are reduced to one or two and in the valley of the Huallaga river (*amaryllis*) they are frequently absent, as in the sympatric *erato favorinus*. In south Brazil the number varies between two and four, and when present the spot between Rs and Cu is more rounded as in *erato*.

HINDWING APICAL CREAM RECTANGLES (Pl. I, fig. 8). The only comparable characters in *melpomene* are the tangential cream rectangles that are continuous with the terminations of the red submarginal arcs of *besckei*.

HINDWING VENTRAL RED ARCS (Pl. I, fig. 8). An effect of red on the hindwing is obtained in the form *besckei* by a row of narrow red submarginal arcs, which lie in intervenal pairs around the posterior border of the hindwing, an effect which seems to be obtained in *erato* by the red raylets of the sympatric *phyllis* and *artifex*.

BODY COLOR. The light parts of the body are normally yellow with white at the base of the antennae and sometimes on the frons and sides of the occiput, but *cytherus* from western Ecuador and *vulcanus* from western Colombia always have the head markings totally white. As occasional specimens from the Amazon basin, the Andean slopes in eastern Ecuador and in the valley of the Huallaga river also have all-white heads and palps, the identification of *erato* and *melpomene* by head color alone is not thoroughly reliable. The palps of *timaretus* are almost entirely black, there being only a very narrow outside line of white scales.

TABLE I. THE PHENOTYPIC CLASSIFICATION OF THE COLOR-PATTERN COMPONENTS IN *Heliconius erato* AND *Heliconius melpomene.*

The code letters refer to the band shapes shown in Text-figures 2 and 3, with the exception of Y, which is an unfigured long band of medium width with a very variable appearance, and the Z-band, which is a broken yellow band with a narrow distal red transverse border. In the other columns, + means present, – means heterozygous, and v means variable. Brackets indicate an approximation only.

| Geographical Locality | Named Form of *erato* | F/W Band | | | | Dennis | Ray | Dorsal Yellow Bar | Ventral Yellow Bar | F/W Yellow Line | H/W White Margin | Iridescence 0-4 | Named Form of *melpomene* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Shape | Red | Yellow | White | | | | | | | | |
| Western Ecuador | *cyrbius*<br>*bellus* | A | + | | | | | | + | | + | 4 | |
| | | A | + | v | + | | | | + | v | + | 3 | *cytherus*<br>*concinnus* |
| | *diformatus* | AB | + | | | | | | + | | + | 4 | |
| | | AB | + | v | v | | | | + | v | + | 3 | *modestus*<br>*sticheli*<br>*tenuistrigus* |
| Western Colombia | *venus* | B | + | | | | | | + | | – | 4 | |
| | | B | + | | | | | | + | v | – | 2 | *vulcanus* |
| Cauca valley | *molinus* | A | + | | | | | | – | | | 3 | |
| | *chestertoni* | | | | | | | + | + | | | 3 | |
| | *nocturnus* | | | | | | | –? | – | | | 3 | |
| Magdalena valley, northern Colombia, Panama and Costa Rica | *colombinus*<br>*antigonus* | C | + | | | | | + | + | | | 1-2 | |
| | | C | + | | | | | + | + | | | 1 | *rosinus* |
| | *guaricus* | C | + | | | | | | – | | | 2 | |
| | | C | + | | | | | | – | | | 1 | *euryas* |
| Panama and Costa Rica | *tristis* | CD | + | | | | | | – | | | 1 | |
| | *juno* | BD | + | | | | | | – | | | 2 | |
| Costa Rica and Mexico | *petiveranus*<br>*demophoon* | D | + | | | | | + | + | | | 0-1 | |
| Eastern Colombia, Venezuela, Trinidad and the Guianas | *hydarus* | (E) | + | | | | | –? | | | | 1 | |
| | *vitellinus* | | | | | | | | | | | | |
| | *adanus* | E | + | | | | | | | | | 1-2 | |
| | | E | + | | | | | | | | | 1 | *melpomene*<br>*flagrans* |

TABLE I. THE PHENOTYPIC CLASSIFICATION OF THE COLOR-PATTERN COMPONENTS IN *Heliconius erato* AND *Heliconius melpomene* (continued).

| Geographical Locality | Named Form of *erato* | F/W Band | | | | Dennis | Ray | Dorsal Yellow Bar | Ventral Yellow Bar | F/W Yellow Line | H/W White Margin | Iridescence 0-4 | Named Form of *melpomene* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Shape | Red | Yellow | White | | | | | | | | |
| Central British Guiana | *magnificus* | (J) | + | | | | | | | | | 3 | |
| Northern Brazil | *rubrizonus*<br>*viculatus* | Y | + | | | | | | | | | 0-1 | |
| | | Y | + | + | | | | | | | | 0 | *luteipictus*<br>*eltringhami*<br>*flavorubrus* |
| | *dryope* | E | + | | | + | | | | | | 0-1 | |
| | | Y | + | v | | + | | | | | | 0 | *dianae*<br>*tyche* |
| | | Y | + | + | | + | | | | | | 0 | *maris* |
| | *erythreus* | EY | + | | | + | + | | | | | 0-1 | |
| | *mixtus* | E | + | | + | + | + | | | | | 0-1 | |
| | *tellus* | E | | + | | + | + | | | | | 0-1 | |
| | | Y | + | + | | + | + | | | | | 0 | *punctarius* |
| | *roseoflavus* | EK | + | + | | + | + | | | | | 0-1 | |
| | *callistus*<br>*belticopis* | K | + | | | | | | | | | 0-1 | |
| | | ZK | + | | | | | | | | | 0 | *melpomenides*<br>*atrosectus* |
| | | ZK | + | + | | | | | | | | 0 | *faivrei*<br>*lucius*<br>*melpinus*<br>*amor*<br>*collis* |
| | *elimeus* | K | + | | | + | | | | | | 0-1 | |
| | | ZK | + | + | | + | | | | | | 0 | *fascinatus*<br>*deinius*<br>*faustinus*<br>*negroidus*<br>*dianides* |

TABLE I. THE PHENOTYPIC CLASSIFICATION OF THE COLOR-PATTERN COMPONENTS IN *Heliconius erato* AND *Heliconius melpomene* (continued).

| Geographical Locality | Named Form of *erato* | F/W Band | | | | Dennis | Ray | Dorsal Yellow Bar | Ventral Yellow Bar | F/W Yellow Line | H/W White Margin | Iridescence 0-4 | Named Form of *melpomene* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Shape | Red | Yellow | White | | | | | | | | |
| Northern Brazil | *andremonus* | K | + | | | + | + | | | | | 0-1 | |
| | *proteus* | K | + | v | v | + | + | | | | | 0-1 | |
| | *androdaixus* | K | + | + | | + | + | | | | | 0-1 | |
| | | ZK | + | + | | + | + | | | | | 0 | *hippolyte*<br>*athalius*<br>*nigroidens*<br>*augustus*<br>*laurentinus*<br>*agalopeius*<br>*stygianus*<br>*majesticus*<br>*lucindellus* |
| | *amalfredus*<br>*helenae* | K | | + | | + | | | | | | 0 | |
| | | K | | + | | + | | | | | | 0 | *cybele*<br>*cybeleius*<br>*eulalius*<br>*funebris*<br>*obscuratus* |
| | *vestus* | K | | + | | | + | | | | | 0 | |
| | *erato*<br>*ledus*<br>*amazonus*<br>*hemicyclus*<br>*oberthuri*<br>*fuliginosus* | K | | + | | + | + | | | | | 0 | |
| | | K | | + | | + | + | | | | | 0 | *thelxiope*<br>*madeirus*<br>*thelxiopeius* |
| | *callicopis* | KN | + | | | | | | | | | 0-1 | |
| | | ZN | + | + | | | | | | + | | 0 | *aphrodyte*<br>*karschi*<br>*lucindus* |
| | *coralii* | KN | + | | | + | | | | | | 0-1 | |
| | | ZN | + | + | | + | | | | | | 0 | *faustalius*<br>*elegantulus* |
| | *udalricus* | KN | + | | | + | + | | | | | 0-1 | |
| | | ZN | + | + | | + | + | | | | | 0 | *rufolimbatus* |

TABLE I. THE PHENOTYPIC CLASSIFICATION OF THE COLOR-PATTERN COMPONENTS IN *Heliconius erato* AND *Heliconius melpomene* (continued).

| Geographical Locality | Named Form of *erato* | F/W Band |  |  |  |  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  |  | Shape | Red | Yellow | White | Dennis | Ray | Dorsal Yellow Bar | Ventral Yellow Bar | F/W Yellow Line | H/W White Margin | Iridescence 0-4 | Named Form of *melpomene* |
| Northern Brazil | *constrictus* | KN |  | + |  | + | + |  |  |  |  | 0 |  |
|  |  | KN |  | + |  | + | + |  |  |  |  | 0 | *perchlorus*<br>*penelopides* |
|  | *lativittus* | LK |  | + |  | + | + |  |  |  |  | 0 |  |
|  |  | L |  | + |  |  |  |  |  |  |  | 0 | *mirabilis* |
|  | *cybelinus* | L |  | + |  | + |  |  |  |  |  | 0 |  |
|  | *estrellus*<br>*emmus*<br>*divus* | L |  | + |  | + | + |  |  |  |  | 0 |  |
|  |  | L |  | + |  | + | + |  |  |  |  | 0 | *cognatus*<br>*rubrus*<br>*agalope*<br>*elevatus* |
|  | *rothschildi* | (L) | v | v | + | + | + |  |  |  |  | 0 |  |
|  | *rosaceus* | GL | + |  | + |  |  |  |  |  |  | 0 |  |
|  |  | GL | + |  | + |  |  |  |  |  |  | 0 | *coronus* |
|  | *ilius*<br>*ochraceus* | GL |  | + |  | + | + |  |  |  |  | 0 |  |
| Valleys of the eastern Ecuadorian Andes | *notabilis* | G | + |  | + |  |  |  |  |  |  | 0 |  |
|  |  | G | + | v | + |  |  |  |  |  |  | 0 | *plesseni*<br>*clytie*<br>*rubricundus*<br>*purus*<br>*adonis*<br>*fraternus* |
|  |  | G | + |  | + | + |  |  |  |  |  | 0 | *neipelti* |
|  | *radiatus*<br>*beatus* | G | + | v | + | + | + |  |  |  |  | 0 |  |
|  |  | G | + | v | + | + | + |  |  |  |  | 0 | *isoldae*<br>*giselae*<br>*iris*<br>*adonides*<br>*rubripictus* |

TABLE I. THE PHENOTYPIC CLASSIFICATION OF THE COLOR-PATTERN COMPONENTS IN *Heliconius erato* AND *Heliconius melpomene* (continued).

| Geographical Locality | Named Form of *erato* | F/W Band | | | | Dennis | Ray | Dorsal Yellow Bar | Ventral Yellow Bar | F/W Yellow Line | H/W White Margin | Iridescence 0-4 | Named Form of *melpomene* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Shape | Red | Yellow | White | | | | | | | | |
| Valleys of the eastern Ecuadorian Andes | *feyeri* | LM | + | | + | + | + | | | | | 0 | |
| | | LM | + | | | + | + | | | | | 0 | *riffarthi* |
| | *etylus* | M | | + | | + | + | | | | | 0 | |
| | | M | | + | | + | + | | | | | 0 | *ecuadorensis* |
| | *agnatus* | M | + | | | + | + | | | | | 0 | |
| | | ELM | + | | | + | + | | | | | 0 | *rubrescens* |
| | | M | + | + | + | | | | | | | 0 | *unimaculatus* |
| Upper River Huallaga | *favorinus* | H | + | | | | | + | + | | | 0 | |
| | | H | + | | | | | + | + | | | 0 | *amaryllis* |
| | *eratophilus* | H | + | | | + | + | + | + | | | 0 | |
| | | H | + | | | + | + | + | + | | | 0 | *melpophilus* |
| Upper River Ucayali-Perené | *microcleus* | I | + | | | | | | | | | 0 | |
| | | I | + | | | | | | | | | 0 | *xenocleus* |
| | | IJ | + | | | | | | | | | 0 | *confluens* |
| River Inambari | *amphitrite*<br>*unipunctatus* | J | + | | | | | | | | | 0 | |
| | | J | + | | | | | | | | | 0 | *euryades* |
| Southwestern Brazil | *cybelellus* | N | | + | | + | | | | | | 0 | |
| | *venustus*<br>*donatius*<br>*telloides* | N | | + | | + | + | | | | | 0 | |
| | | N | | + | | + | + | | | | | 0 | *vicinus*<br>*penelope*<br>*noctis* |
| | *sanguineus*<br>*confluens* | N | + | | | + | + | | | | | 0 | |
| | *henrici* | N | + | + | | + | + | – | – | | | 0 | |
| | | N | | + | | + | + | – | – | + | | 0 | *margaritae* |
| | | N | + | | | + | + | + | + | | | 0 | *penelemandae* |
| | | N | + | + | | + | + | + | + | | | 0 | *penelopeiae* |
| | *leonorae* | KL | + | | | + | + | – | – | + | | 0 | |
| | | ZK | + | + | | + | + | + | + | + | | 0 | *excellens* |
| | | ZN | + | + | | + | + | + | + | + | | 0 | *amneris*<br>*carneus* |

TABLE I. THE PHENOTYPIC CLASSIFICATION OF THE COLOR-PATTERN COMPONENTS IN *Heliconius erato* AND *Heliconius melpomene* (continued).

| Geographical Locality | Named Form of *erato* | F/W Band | | | | Dennis | Ray | Dorsal Yellow Bar | Ventral Yellow Bar | F/W Yellow Line | H/W White Margin | Iridescence 0-4 | Named Form of *melpomene* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Shape | Red | Yellow | White | | | | | | | | |
| Southwestern Brazil | | ZN | + | + | | | | + | + | + | | 0 | *biedermanni* |
| | | ZN | + | | | | | + | + | + | | 0 | *amandae* |
| | *speratus* | N | + | + | | | | – | | | | 0 | |
| | | N | + | + | | | | – | – | | | 0 | *flammeus* |
| | *diffluens* | NF | + | | | | | + | + | + | | 0 | |
| | | NF | + | + | | | | – | – | + | | 0 | *amandoides* |
| | *flavomixtus* | | | | | | | | | | | | |
| | *anactorie* | NF | + | + | | + | + | | | + | | 0 | |
| | *simplex* | LF | + | | | | | | | | | 0 | |
| | *palmatus* | LF | + | | | + | + | | | | | 0 | |
| | *anacreon* | LF | + | | | + | + | + | + | + | | 0 | |
| | | LF | + | | | + | + | + | + | + | | 0 | *curvifascius* |
| | | | | | | | | | | | | | *aidae* |
| | *anacreonides* | | | | | | | | | | | | |
| | *krugeri* | LF | + | | | + | + | –? | –? | + | | 0 | |
| | *amatus* | | | | | | | | | | | | |
| | *athene* | LF | + | | | | | – | – | + | | 0 | |
| | | LF | + | + | | | | – | – | | | 0 | *obscurifascius* |
| | *ottonis* | LF | | + | | + | + | + | + | + | | 0 | |
| | *differens* | LF | | + | | + | + | | | | | 0 | |
| | *celiae* | F | + | | + | + | + | – | – | + | | 0 | |
| | *anaitis* | F | + | | | | + | + | + | + | | 0 | |
| | *phyllidis* | F | + | | | | | – | – | + | | 0 | |
| Southern and eastern Brazil | *phyllis* | | | | | | | | | | | | |
| | *artifex* | F | + | | | | | + | + | + | | 0 | |
| | | F | + | | | | | + | + | + | | 0 | *nannus* |
| | | | | | | | | | | | | | *besckei* |
| Hybridization zone in southern Colombia | *glaucinus* | CL | + | | | | | | – | | | 0 | |
| | | ZK | + | | + | | | | | | | 0 | *annae* |
| | | ZK | + | + | | | | | | | | 0 | *parvus* |
| | *problematus* | CL | + | | | + | + | –? | –? | | | 0 | |
| | | ZK | + | | + | + | + | | | | | 0 | *gratiosus* |
| | | ZK | + | + | | + | + | | | | | 0 | *dione* |
| | | | | | | | | | | | | | *aurofasciatus* |
| | | ZK | + | + | | + | + | – | | | | 0 | *paulae* |
| | *meliorinus* | CL | | + | | + | + | + | + | | | 0 | |
| | *perplexus* | NL | + | | | + | + | + | + | | | 0 | |
| | *dignus* | E | + | | | | | + | + | | | 0 | |

TABLE I. THE PHENOTYPIC CLASSIFICATION OF THE COLOR-PATTERN COMPONENTS IN *Heliconius erato* AND *Heliconius melpomene* (continued).

| Geographical Locality | Named Form of *erato* | F/W Band | | | | Dennis | Ray | Dorsal Yellow Bar | Ventral Yellow Bar | F/W Yellow Line | H/W White Margin | Iridescence 0-4 | Named Form of *melpomene* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Shape | Red | Yellow | White | | | | | | | | |
| Above 1,250 meters in the eastern Ecuadorian Andes | | ZN | | + | | | | | | | | 0 | *timoretus* |
| | | ZN | + | + | | | + | | | | | 0 | *virgatus* |
| | | | | | | | | | | | | | *insoletus* |
| | | | | | | | | | | | | | *contiguus* |
| | | | | | | | | | | | | | *peregrinus* |
| | | ZN | + | + | | + | + | | | | | 0 | *richardi* |
| | | ZN | + | + | | | | | | + | | 0 | *erebius* |
| | | ZN | + | + | | | | + | | | | 0 | *pluto* |

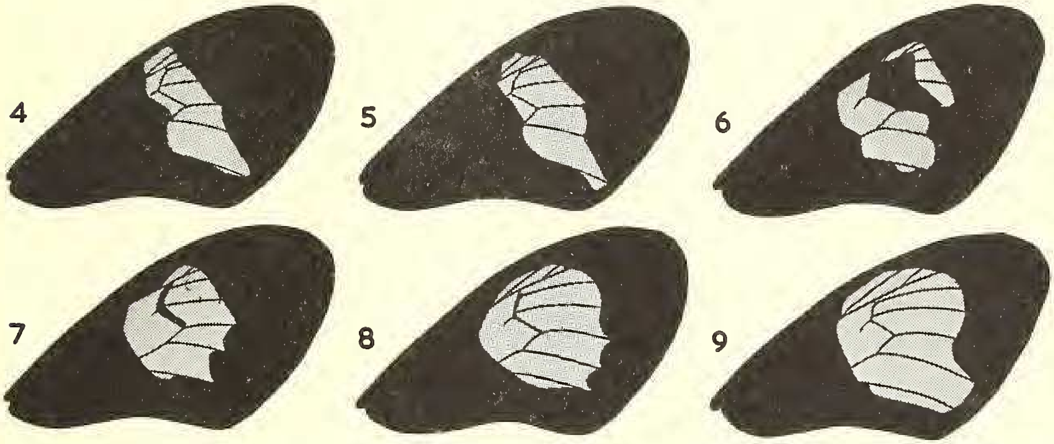
## IV. GENETICAL EXPERIMENTS

In the context of these investigations the location of the New York Zoological Society's tropical research station in Trinidad is most fortunate, for while on the neighboring continent there is polymorphism and a high degree of variability, in Trinidad both *Heliconius erato* and *melpomene* are monomorphic and relatively constant. For this reason, and that of convenience, the Trinidad stocks have been used as a datum for comparison with material from western and eastern Ecuador. The experimental work, though performed as material was available, is here presented in two parts, the first involving *erato* and the second *melpomene.*

### *Heliconius erato*

The named geographical subspecies used were *Heliconius erato cyrbius* Godart 1819 from Ecuador west of the Andes, *H. erato adanus* Seitz 1913 from Trinidad and *H. erato notabilis* Salvin & Godman 1868 from Ecuador east of the Andes. *Cyrbius* is figured in color in Seitz (1913) Plate 78 a; *notabilis* is figured in color in Eltringham (1916) Plate xii, figure 7; and though not known to be figured in color, *adanus* is similar to *dryope,* which is reproduced in Seitz (1913) on Plate 78 b, but without dennis.

As wild fertilized females of *cyrbius* and *notabilis* were collected on the first and subsequent trips respectively, it was possible to maintain



TEXT-FIGS. 4-9. Dorsal views of right forewings of laboratory-bred hybrids to show shape of bands. Text-fig. 4, $F_1$ of *cyrbius* × *adanus* (*erato*). Text-fig. 5, $F_1$ of *cytherus* × *flagrans* (*melpomene*). Text-fig. 6, $F_1$ of *notabilis* × *adanus* (*erato*), showing divided truncate band. Text-fig. 7, $F_2$ of *notabilis* × *adanus,* showing short semidivided truncate band. Text-fig. 8, similar $F_2$ showing short semidivided round tip band. Text-fig. 9, similar $F_2$ showing long undivided round tip band. Approximately 1½ times natural size.

pure stocks of both these Ecuadorian forms as well as the endemic *adanus.*

Field observations in the locality from which *cyrbius* was obtained showed that it is essentially monomorphic, though it is subject to minor variation in the width of the red forewing band, the width and density of the hindwing ventral yellow bar and the presence and development of the forewing costal spot. Variation in the width and density of the hindwing white margin is common only at the northern limits of its range.

In the locality from which *notabilis* was obtained it is also monomorphic, and though relatively constant in the size of the forewing double bands, it is variable in the relative proportions of red to white within them and in the distance by which they are separated. One example was taken in a total of about fifty in which the outer band is represented only by the inner half of the normally oval band, a condition referred to later as "truncate." Two such specimens are in the Joicey collection from the same locality.

## SECTION A: WESTERN ECUADORIAN *cyrbius* AND TRINIDADIAN *adanus*

### First Experiment: *cyrbius* × *adanus*

Reciprocal crosses were performed between the progeny of two wild fertilized *cyrbius* females brought back from western Ecuador and laboratory-reared Trinidadian stock *adanus.* Both sexes of all the progeny were reasonably uniform. The phenotypic characters of the parental and $F_1$ generations are summarized in Table II, though only only those characters in which the parents differed are included.

*Expansion*—The intermediate red band of the $F_1$ generation may be compared with those of the parents in Text-figures 2A, 2E & 4. It is interesting to notice that the $F_1$ band is similar to the wild form from northern Colombia (Text-fig. 2C), which is an intermediate geographical position.

The intermediate blue iridescence is also comparable with that occurring wild in northern Colombia, though the local wild variation never approaches the extremes shown by these experimental parents.

The hindwing ventral yellow bar is represented in the $F_1$ by an area which is similar in location to yellow bar, but which is differentiated from the normal brown ventral ground-color by appearing unusually shiny when examined by light reflected at low angles. It can be seen most easily by holding the insect upside down beneath a light source and altering the angle at which the wing is viewed. Museum collections contain many specimens which show this condition from Panama and from between the western and eastern cordilleras of northern Colombia, but beyond the extremities of the cordilleras it is a rarity. It is known also from Bolivia.

The hindwing white margin is represented in the $F_1$ by a peripheral border of intervenal terminal white scales which is variable in its completeness. In addition, there is a barely perceptible differentiation which is similar in texture to the $F_1$ hindwing bar over the border of the hindwing that bears the white margin in the Ecuadorian parent.

The light parts of the head pattern are principally yellow, but the palps grade from distally

TABLE II.

| | PHENOTYPIC CHARACTERS | | |
|---|---|---|---|
| | Parents | | |
| | *cyrbius* | *adanus* | $F_1$ Generation |
| Ground Color | Bright blue iridescence | Dull blue iridescence | Intermediate blue iridescence |
| Hindwing White Margin | Well developed | Absent | Intermittent peripheral white scales and a differentiated border |
| Hindwing Ventral Yellow Bar | Well developed | Absent | Slight differentiation of ground color |
| Forewing Red Band | Narrow and short | Broad and long | Intermediate in both dimensions |
| Light Head Color | White | 90% yellow<br>10% white | 70% yellow<br>30% white |
| Forewing Costal Spot | Absent (in parents) | Present but variable | Variably present or absent |

yellow to proximally 50% yellow and the latero-posterior aspects of the occiput are white. There is also a little more white on the vertex than is normal for the Trinidadian parent.

The forewing costal spot may be expressed in the $F_1$ generation. From the first experiment it may be concluded that:

1. There is no dominance between the broadness and narrowness of the *adanus* and *cyrbius* forewing bands.
2. There is no dominance between the longness and shortness of the *adanus* and *cyrbius* forewing bands.
3. There is no dominance between the blue iridescence of *cyrbius* and the dull iridescence of *adanus*.
4. The absence of hindwing white margin is semidominant to its presence.
5. The absence of hindwing ventral yellow bar is semidominant to its presence as expressed by *cyrbius*.
6. There is no dominance between the whiteness and yellowness of the light head markings of *cyrbius* and *adanus*.

### Second Experiment: Backcrosses to *cyrbius* and *adanus*

In the backcrosses to the *cyrbius* and *adanus* stocks it was not possible to use the original male parents because they had died, but as both parental populations are reasonably constant the results yield good data. A summary of the phenotypic characters of the progeny is shown in Tables III and IV.

*Expansion*—Of interest is the fact that all characters may be expressed by both sexes, indicating that the sex-chromosomes are not involved and there is no evidence for sex-limitation.

It was not possible to score iridescence, for though there was considerable variation it seemed continuous within limits which were far less extreme than those of the parents.

The scoring of forewing band was similarly unsatisfactory, but this difficulty was overcome by measuring the length and breadth of the band in relation to wing width, though the results will be considered later together with those of the $F_2$ generation produced by the third experiment.

From the second experiment it may be concluded that the characters being studied are carried on the autosomes, so the sex of the progeny will not be recorded in succeeding tables.

### Third Experiment: (*cyrbius* × *adanus*) × (*cyrbius* × *adanus*)

The phenotypic classification of the progeny of two brother × sister $F_1$ crosses is shown in Table V.

*Expansion*—The data from the backcrosses and from the $F_2$ generation are consistent with head color, hindwing ventral yellow bar and hindwing white margin each being controlled by a single pair of allelomorphs. The evidence for this is the near equality of the proportions of each class in the backcrosses and the reasonable approximation to 1:2:1 in the $F_2$. The chief discrepancy in this hypothesis is the apparent heavy weighting of the *cyrbius* class of head color in the backcross to *cyrbius* (Table III), but as the original male was not available and as only two backcrosses were made to *cyrbius* it is quite possible that the genetic background has shifted this difficult character towards the scoring of an excess of *cyrbius*-type individuals. Even so the data are not significantly inconsistent with the theoretical 1:1 proportions. Though unmeasured, the higher degree of variability of both hindwing ventral yellow bar and white margin in the $F_2$ suggests that modifiers are present in the *cyrbius* stock.

The data suggest that costal spot is inherited by a single pair of allelomorphs with presence of spot semi-dominant to its absence. Owing to the difficulty of identifying the heterozygotes with certainty, the spot class has been bulked for comparison with non-spot. The approximation to 3:1 ratios in the backcross to *adanus* and in the $F_2$ are consistent with this hypothesis if the *adanus* parents and the $F_1$ used were heterozygous for this character. This is plausible as non-spot occurred in the *adanus* stock at an unmeasured but low frequency. This potential heterozygosity in *adanus* accounts for interbrood variation in performance in the $F_1$ when crossed with the homozygous phenotypically non-spot *cyrbius*.

For the estimation of linkage, the number of recombinations of all the characters under consideration have been presented in Table VI.

The data give highly significant evidence for linkage between hindwing ventral yellow bar and hindwing white margin ($P = 0.001$). The maximum likelihood estimate for the crossover value is 14.4% ± 1.22% assuming no misclassification of the phenotypes. If there is a small degree of misclassification, then this estimate would be too high. This event is not unlikely, for the distinction between heterozygous bar and homozygous non-bar, and between heterozygous margin and homozygous non-margin, are in some instances extremely difficult to perceive.

There is no evidence for linkage between the genes controlling head color and either stripe or

TABLE III.

| Brood | Parentage | | Phenotype of Progeny | | | | | | | | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Hindwing Yellow Bar | | Hindwing White Margin | | Head Color | | Forewing Costal Spot | | |
| | | | *cyr.* | $F_1$ | *cyr.* | $F_1$ | *cyr.* | $F_1$ | *cyr.* | $F_1$ | |
| C14A | $F_1$ (*cyrbius* × *adanus*) ♂ × *cyrbius* ♀ | ♂ | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 |
| | | ♀ | 3 | 1 | 3 | 1 | 3 | 1 | 4 | 0 | 4 |
| Total | | | 3 | 2 | 3 | 2 | 4 | 1 | 4 | 1 | 5 |
| C13 | $F_1$ (*cyrbius* × *adanus*) ♀ × *cyrbius* ♂ | ♂ | 4 | 5 | 4 | 5 | 6 | 3 | (5) | (2) | 9 |
| | | ♀ | 3 | 5 | 3 | 5 | 6 | 2 | (3) | (3) | 8 |
| Total | | | 7 | 10 | 7 | 10 | 12 | 5 | (8) | (5) | 17 |
| Addition of C14A and C13 | | | 10 | 12 | 10 | 12 | 16 | 6 | (12) | (6) | 22 |

TABLE IV.

| Brood | Parentage | | Phenotype of Progeny | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Hindwing Yellow Bar | | Hindwing White Margin | | Head Color | | Forewing Costal Spot | | |
| | | | *adanus* | $F_1$ | *adanus* | $F_1$ | *adanus* | $F_1$ | Pres. | Absent | Total |
| C5A | $F_1$ (*cyrbius* × *adanus*) ♂ × *adanus* ♀ | ♂ | 4 | 8 | 4 | 8 | 7 | 5 | 9 | 3 | 12 |
| | | ♀ | 4 | 4 | 2 | 6 | 4 | 4 | 7 | 1 | 8 |
| | | Total | 8 | 12 | 6 | 14 | 11 | 9 | 16 | 4 | 20 |
| C2 | $F_1$ (*cyrbius* × *adanus*) ♀ × *adanus* ♂ | ♂ | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 |

margin, nor is there conclusive evidence of linkage between costal spot and any other character studied, but the data are insufficient to deny that there is any linkage.

The forewing bands of the laboratory populations of the parental *cyrbius* and *adanus* stocks and those of their $F_1$ and $F_2$ progeny were measured for variation in width and length. The data, corrected for variation in wing size, are presented in Text-figs. 10 – 12 and 13 – 15, with similar data for *melpomene*. The most outstanding features of the $F_2$ data to be noticed at this stage are the unimodal distribution, the near complete absence of parental classes for both measurements and the location of the mode midway between those of the parental populations. The data from the back crosses (not figured) also produce a distribution with modes midway between those of the $F_1$ and appropriate parental population. Of interest too is the in-

TABLE V.

| Brood | Parentage | Phenotype of Progeny | | | | | | | | | | | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Hindwing Yellow Bar | | | Hindwing White Margin | | | Head Color | | | Forewing Costal Spot | | |
| | | *cy.* | $F_1$ | *ad.* | *cy.* | $F_1$ | *ad.* | *cy.* | $F_1$ | *ad.* | Present (*ad.*+$F_1$) | Absent *cy.* | |
| C4 | $F_1$ (*cyrbius* × *adanus*) ♂ × $F_1$ (*cyrbius* × *adanus*) ♀ | 3 | 8 | 7 | 3 | 9 | 6 | 4 | 10 | 4 | 15 | 3 | 18 |
| C12 | Replicate of C4 | 2 | 4 | 2 | 2 | 5 | 1 | 2 | 2 | 4 | 6 | 2 | 8 |
| | Total | 5 | 12 | 9 | 5 | 14 | 7 | 6 | 12 | 8 | 21 | 5 | 26 |

TABLE VI.

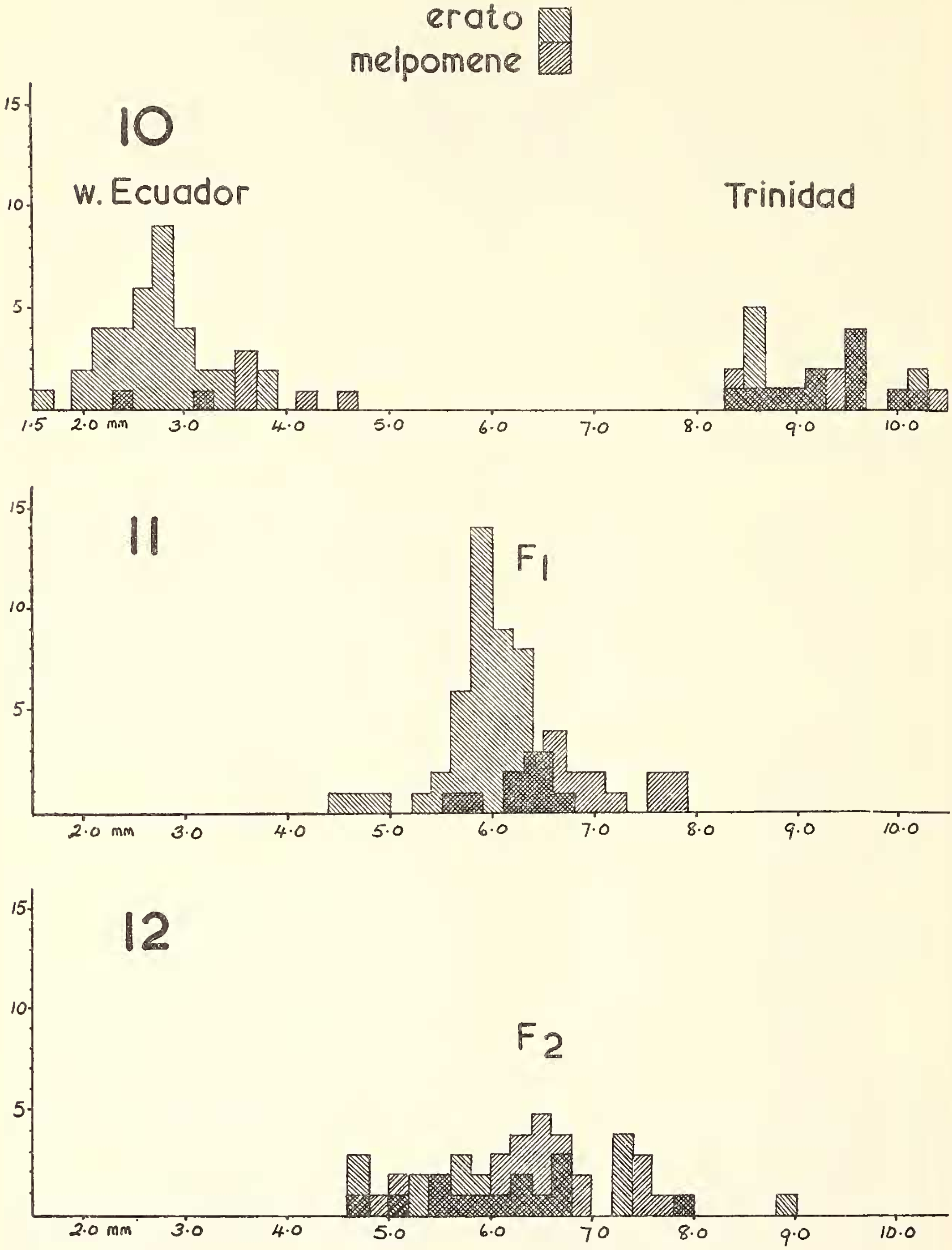
| | | | Number of Recombinations of Characters in Progeny of *cyrbius* and *adanus* | | | | | |
|---|---|---|---|---|---|---|---|---|
| Brood | Parentage | Nos. of Specimens | Head Color & H/W Yellow Bar | Head Color & H/W White Margin | H/W Yellow Bar & H/W White Margin | Head Color & F/W Costal Spot | H/W Yellow Bar & F/W Costal Spot | H/W White Margin & F/W Costal Spot |
| C13 | $F_1$ Backcross to *cyrbius* | 17 | 9 | 9 | 0 | 2 (out of 13 specimens scored) | 8(13) | 8(13) |
| C14A | $F_1$ Backcross to *cyrbius* | 5 | 3 | 3 | 0 | 2 | 3 | 3 |
| C5A | $F_1$ Backcross to *adanus* | 20 | 11 | 10 | 5 | 3 | 3 | 3 |
| C4 | (*adanus* × *cyrbius*)$F_2$ | 18 | 10 | 11 | 5 | 3 | 6 | 6 |
| C12 | (*adanus* × *cyrbius*)$F_2$ | 8 | 6 | 6 | 1 | 2 | 2 | 2 |

creased degree of variation in the $F_2$ measurements when compared with the $F_1$ or either parental stock. One may conclude that both the width and the length of the band in western Ecuador and Trinidad are either under polygenic control with little or no dominance or there are an approximately equally large number of dominant genes in each race. The gradual change in the dimension of the forewing band between western Ecuador and Central America and Trinidad is consistent with these data, though most sudden change takes place between western Ecuador and western Colombia.

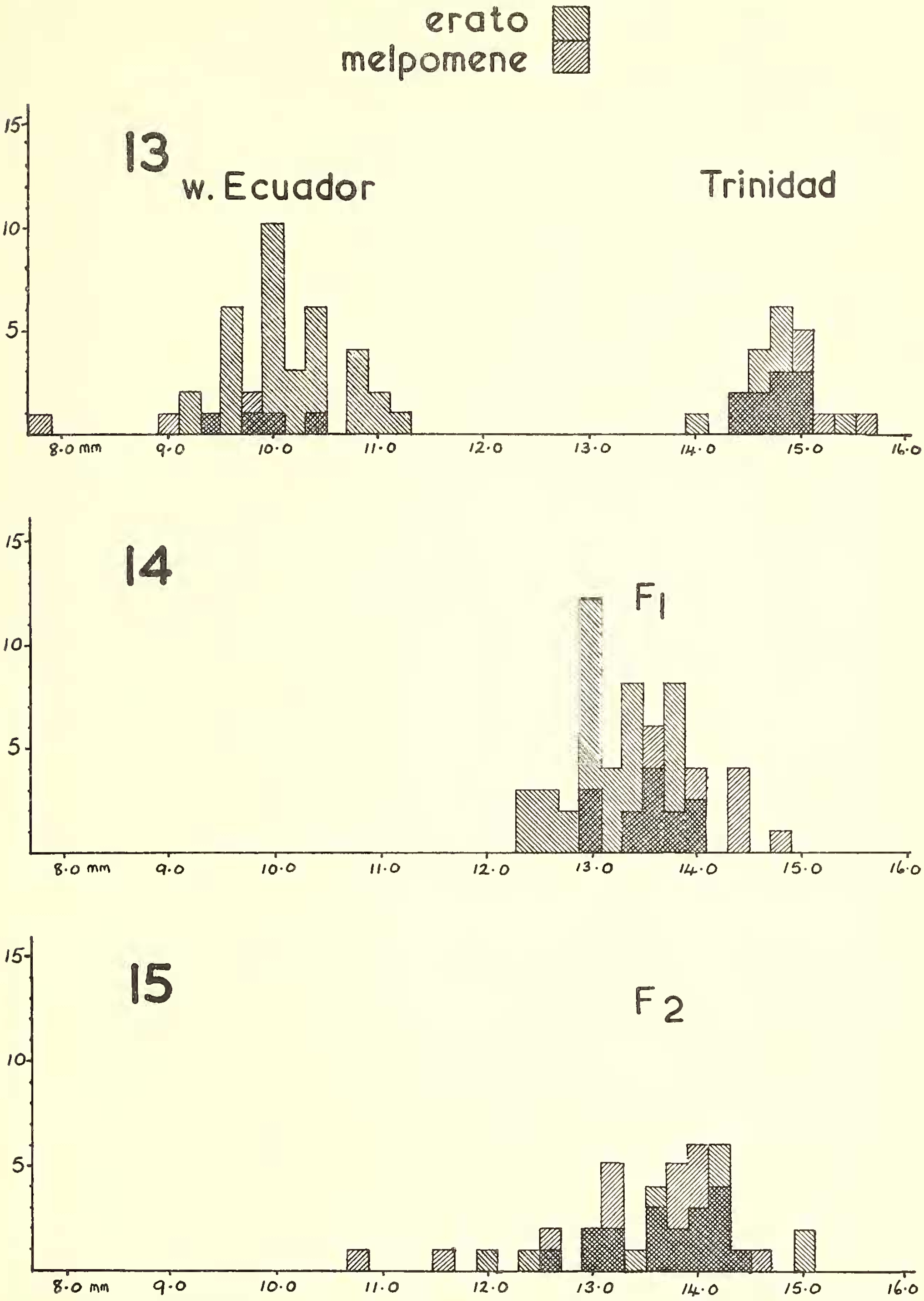
## SECTION B: EASTERN ECUADORIAN *notabilis* AND TRINIDADIAN *adanus*

### Fourth Experiment: *notabilis* × *adanus*

Reciprocal crosses were performed between pure stock males and females of *notabilis* from eastern Ecuador and *adanus* from Trinidad, but only fourteen $F_1$ individuals were produced because they were reared at a time of peak disease incidence. As the parental types differed only in respect of iridescence, forewing band and costal spot, these were the only characters studied and are recorded in Table VII.



Text-figs. 10-12. Frequency histograms demonstrating variation in band shape in *H. erato* and *H. melpomene*. Text-fig. 10—variation in band-width in the western Ecuadorian and Trinidadian parents; Text-fig. 11—variation in their $F_1$ progeny; Text-fig. 12—variation in the $F_2$ progeny. The vertical axes show numbers of individuals and the horizontal axes give measurements in mm. corrected to a standard wing-length of 16 mm.



TEXT-FIGS. 13-15. Frequency histograms demonstrating variation in band shape in *H. erato* and *H. melpomene.* Text-fig. 13—variation in band-length in the western Ecuadorian and Trinidadian parents; Text-fig. 14—variation in their $F_1$ progeny; Text-fig. 15—variation in the $F_2$ progeny. The vertical axes show numbers of individuals and the horizontal axes give measurements in mm. corrected to a standard wing-length of 16 mm.

TABLE VII.

| | Phenotypic Characters | | |
|---|---|---|---|
| | Parents | | $F_1$ Generation |
| | *notabilis* | *adanus* | |
| Ground Color | Matt black | Dull blue | Just perceptible blue |
| Forewing Band | Red, white and yellow | Red | Red |
| | Double | Single | Variably intermediate |
| | Short | Long | Short |
| Forewing Costal Spot | Absent | Variably present or absent | Variably present or absent |

*Expansion*—The iridescence of the $F_1$ generation was barely perceptible and in subsequent experiments was impossible to score, for the iridescence of *adanus* is only slight and the difference between the $F_1$ and either parent could not be detected with certainty.

The striking variability of the $F_1$ forewing band was due to variation in the shape of the tip and the degree of division of the band over the apex of the discal cell. The classification of the $F_1$ generation with respect to the tip shape and division of band is presented in Table VIII.

Though the $F_1$ forewing bands have been classified into "divided" and "semi-divided," it seems likely that with a larger sample the discretion of the classes would break down into more continuous variation. The semi-divided band has only a black line along the transverse vein at the apex of the discal cell (Text-fig. 8) but the divided band (Text-fig. 6) has a variable but appreciable quantity of black scales on the membrane immediately distal to the apex of the discal cell, which separates the band into two to a variable degree.

In all the 14 $F_1$ specimens the band length was only a little greater than that of the *notabilis* parent, and appreciably shorter than that of *adanus*.

The forewing bands of the $F_1$ were also divisible into a class in which the apex of the band

TABLE VIII.

| Brood | Parentage | Phenotypic characters of $F_1$ progeny | | | | |
|---|---|---|---|---|---|---|
| | | Semidivided | | Divided | | Total |
| | | Round | Truncate | Round | Truncate | |
| C18 | Round tip *notabilis* ♀ × *adanus* ♂ | 0 | 2 | 4 | 3 | 9 |
| C14B | Replicate of C18 | 0 | 0 | 0 | 3 | 3 |
| C11 | Round tip *notabilis* ♂ × *adanus* ♀ | 0 | 1 | 0 | 0 | 1 |
| C5B | Replicate of C11 | 0 | 0 | 0 | 1 | 1 |
| | Total | 0 | 3 | 4 | 7 | 14 |

was rounded, as in Text-fig. 8, or one in which the tip was truncate, as in Text-fig. 7. The female parent of brood C 18 was phenotypically round though the progeny contained five truncate and four round tipped individuals. Bearing in mind that the female is the heterogametic sex in Lepidoptera, the presence of round and truncate bands in both sexes of the progeny of reciprocal crosses enables sex-linkage and sex-limitation to be disregarded. For this reason the sexes are not included in the tables.

The $F_1$ forewing bands were all red even though the band of *notabilis* has red, white and yellow scales.

Forewing costal spot is of variable occurrence in wild *notabilis* but was absent in the experimental parents. It was variable in both *adanus* and the $F_1$.

From the fourth experiment it may be concluded that:

1. Shortness in *notabilis* band is semidominant or dominant to longness in *adanus*.
2. The inheritance of division of band is complex.
3. Red is dominant to yellow and white.
4. There is no dominance between the dull iridescence of *adanus* and the matt black of *notabilis*.

### Fifth Experiment: Backcrosses to *notabilis* and *adanus*

There were three successful backcross matings to *adanus*, the progeny of which are classified in Table IX, but only one adult emerged from the several attempted backcrosses to *notabilis*. In the backcrosses to *notabilis* and *adanus* stocks it was not possible to use the original male parents because they had died.

### Sixth Experiment (*notabilis* × *adanus*) × (*notabilis* × *adanus*)

Again owing to disease only one offspring was produced; its characters are described in Table X.

*Expansion*—The near equality of the long and short-banded classes in the backcross progeny of broods C16, C6 and C7 suggests that only a single pair of allelomorphs is involved. The near-short length of the $F_1$ band and the recovery of the short band in the solitary backcross to *notabilis* (C19) and $F_2$ (C15) confirms that shortness is semidominant to longness.

The near equality of the truncate tip and round tip classes in the same backcross progeny are also consistent with control by a single pair of allelomorphs. The absence of round tip in any known *adanus* crosses not involving *notabilis*,

TABLE IX.

| Brood | Phenotypic Characters | | | | | |
|---|---|---|---|---|---|---|
| | Parents | Progeny | | | | |
| | | Long Band | | Short Band | | |
| | | Round Tip | Truncate Tip | Round Tip | Truncate Tip | Total |
| C16 | Round tip, semidivided<br>$F_1$ (*notabilis* × *adanus*) ♂<br>×<br>*adanus* ♀ | 7 | 8 | 8 | 4 | 27 |
| C7 | Same male as in C16<br>×<br>*adanus* ♀ | 14 | 16 | 10 | 7 | 47 |
| C6 | Round tip, divided<br>$F_1$ (*notabilis* × *adanus*) ♀<br>×<br>*adanus* ♂ | 2 | 2 | 2 | 4 | 8 |
| | Total | 23 | 26 | 20 | 15 | 84 |
| C19 | Truncate tip, undivided<br>$F_1$ (*notabilis* × *adanus*) ♀<br>×<br>Fully divided, round tip<br>*notabilis* ♂ | One ♀, double short band, truncate tip, red, white and yellow | | | | |

TABLE X.

| Brood | Parentage | Phenotypic Characters of Progeny |
|---|---|---|
| C15 | (*notabilis* × *adanus*) ♂<br>undivided round tip<br>×<br>(*notabilis* × *adanus*) ♀<br>undivided round tip | 1 ♂, with double short band, round tip, red with a few yellow and white scales anteriorly |

and the appearance of both round and truncate tip in the $F_1$ progeny, suggest the eastern Ecuadorian *notabilis* parents were heterozygous for this character. As they were phenotypically round-tipped the truncate-tipped condition must be recessive. Phenotypic truncate tip, which on present evidence is the homozygous recessive condition, is known from the parental *notabilis* locality but at very low frequency. In a sample of just over fifty wild specimens, only one was of this type. The frequency of the heterozygotes can be calculated as 27%, so the chance of heterozygotes being captured for establishing the breeding stocks was reasonable. There were very few emergences in the laboratory pure stock $F_1$ broods and no phenotypically truncate-tipped progeny were noticed.

In the backcross progeny C16, C7 and C6, all the long-banded forms, whether truncate or not, showed no division of the band at all (Text-fig. 9). All the short banded forms, both truncate and round, had the band divided by a variably broad transverse strip of ground color emanating distally from the apex of the discal cell (Text-figs. 7 & 8). This 100% association of long band and lack of division indicates either that both characters are under the control of one gene or that the two genes responsible are very closely linked. Judging by the variability in the performance of the factor for division in the $F_1$, it is semirecessive and probably multifactorially modified in the *notabilis* population.

An examination of the data from broods C16, C7 and C6 revealed no evidence of linkage between tip shape and band length.

The *adanus* and $F_1$ parents of Brood C7 each had a weak costal spot and the scored progeny segregated into 10 strong spot, 23 weak and 8 non-spot. This is consistent with a 1:2:1 ratio, suggesting that each parent was heterozygous for semi-dominant spot. Brood C16 was the progeny of a weak spot $F_1$ and a strong spot *adanus*, and all the 26 scored individuals had a variably strong costal spot. This would be the expected result of the homozygous dominant crossed with its heterozygote. These data support that derived from the *cyrbius* crosses, and suggest that costal spot in *erato* is controlled by a single pair of allelomorphs with spot semi-dominant to non-spot.

### *Heliconius melpomene*

It was intended that exactly comparable crosses would be performed with *melpomene* as with *erato*, but due to deaths from virus disease these were not possible.

The subspecies used were strictly sympatric with the *erato* used and have been named *Heliconius melpomene cytherus* Hewitson 1869 from Ecuador west of the Andes, *H. melpomene plesseni* Riffarth 1907 from Ecuador east of the Andes and *H. melpomene flagrans* Stichel 1919 from Trinidad.

As only one wild male *cytherus* was brought back from the single trip to western Ecuador, it was not possible to maintain pure stocks of this form. In its locality it appears subject to variation only in the development of the white hindwing margin and the forewing white flecks.

### SECTION A: WESTERN ECUADOR *cytherus* AND TRINIDADIAN *flagrans*

#### Seventh Experiment: *cytherus* × *flagrans*

Only one successful mating was achieved between the *cytherus* male and Trinidadian females. The phenotypic characters of the parental and $F_1$ generations are summarized in Table XI.

*Expansion*—The intermediate red band of the $F_1$ is subject to very little variation and may be compared with the parental bands in Text-figs. 3A, 3E & 5, and comparison with Text-fig. 3C shows that it is also similar to that occurring wild in northern Colombia, which is an intermediate geographical location.

The white flecks, which are characteristic of the *cytherus* forewing band, did not appear in any $F_1$ individuals.

The blue iridescence is also intermediate in intensity and again similar to that occurring in the valleys of northern Colombia, though, as in *erato*, the local variation there is far less than the difference between the experimental parental characters.

TABLE XI.

| | Phenotypic Characters | | |
|---|---|---|---|
| | Parents | | $F_1$ Generation |
| | *cytherus* | *flagrans* | |
| Ground Color | Bright blue iridescence | Dull blue iridescence | Intermediate blue iridescence |
| Hindwing White Margin | Broad and complete | Intermittent peripheral scales only | Peripheral scales more complete and differentiated border |
| Hindwing Ventral Yellow Bar | Well developed | Absent | Slight differentiation of ground color |
| Forewing Red Band | Narrow and short | Broad and long | Intermediate in both dimensions |
| Light Head Color | 5% yellow<br>95% white | 95% yellow<br>5% white | 90% yellow<br>10% white |
| Forewing Costal Spot | Absent (in parent) | Present | Present |
| Forewing White Fleck | Present | Absent | Absent |
| Forewing Yellow Line | Absent (in parent) | Absent | Absent |

The hindwing ventral yellow bar is exactly comparable to that expressed in the *erato* $F_1$, in that it is an area which is similar in size and shape to bar, but differentiated from the ground color not by color but by reflectance.

The hindwing white margin is represented by an intervenal peripheral fringe of white scales which encroach onto the membrane to a variable but very limited extent, though the area occupied by the white margin in the Ecuadorian parent is differentiated by abnormal reflectance. As the parents from Trinidad have some peripheral scales of white, the $F_1$ with minimal white fringe is distinguishable from pure *flagrans* stock, only by the "shadow" of the broad margin.

The light markings of the head and thorax, when compared with *flagrans*, show only a slight reduction of yellow.

The forewing costal spot is fully expressed in the $F_1$ generation.

From the first experiment it may be concluded that:

1. There is no dominance between broadness and narrowness of the *flagrans* and *cytherus* forewing bands.

2. There is no dominance between the longness and shortness of the *flagrans* and *cytherus* forewing bands.

3. There is no dominance between the blue iridescence of *cytherus* and the dull iridescence of *flagrans*.

4. The absence of hindwing white margin is semidominant to its presence.

5. The absence of hindwing ventral yellow bar is semidominant to its presence as expressed by *cytherus*.

6. Preponderance of yellow head color is semidominant to preponderance of white head color.

7. The presence of forewing costal spot as expressed by *flagrans* is dominant to its absence.

8. The presence of forewing white fleck is recessive to its absence.

### Eight Experiment: Backcrosses to *cytherus* and *flagrans*

Owing to disease the successful matings between the $F_1$ females and the original western Ecuadorian male parent produced only three progeny, the characters of which are recorded in Table XII.

TABLE XII.

| Brood | Parentage | | F/W Yellow Line | | H/W Yellow Bar | | H/W White Margin | | Forewing Fleck | | Head Color | | Costal Spot | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $F_1$ (*cytherus* × *flagrans*) ♀ | | *cy.* | $F_1$ | *cy.* | $F_1$ | *cy.* | $F_1$ | *cy.* | $F_1$ | *cy.* | $F_1$ | *cy.* | $F_1$ | Total |
| $F_1BX$ | × *cytherus* ♂ | ♂ | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 |
| | | ♀ | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 |
| M5 | Replicate of $F_1BX$ | ♀ | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 |

### Ninth Experiment: (*cytherus* × *flagrans*) × (*cytherus* × *flagrans*)

The phenotypic classification of the progeny is presented in Table XIII. The small number in the backcross broods $F_1BX$ and M5 are unfortunate but the $F_2$ data are sufficiently large, and bear a sufficiently close resemblance to a 1:2:1 ratio, for hindwing ventral yellow bar, hindwing white margin and proportions of white on the head each to be assumed to be controlled by a single pair of allelomorphs showing incomplete dominance. Costal spot, which is present in both *flagrans* and the $F_1$, bears a reasonable relationship to a 3:1 ratio in the $F_2$, which is consistent with the hypothesis that it is controlled by a pair of allelomorphs with presence of costal spot dominant. A similar situation pertains in forewing yellow line, except the absence of line is dominant and forewing fleck is probably also controlled by a pair of allelomorphs with its absence dominant. The male Ecuadorian parent must have been heterozygous for forewing yellow line, but being recessive it was not phenotypically expressed.

Measurements of the width and length of the forewing band in the parental, $F_1$ and $F_2$ generations were taken, corrected for a standard wing width, and plotted on the same histograms that portray the data in *erato,* (Text-fig. 10 — 15). Just as in *erato,* the unimodal curve of variation in the $F_2$, the greater variance in the $F_2$ when compared with the $F_1$ and the lack of parental classes of measurement in the $F_2$, all point to multifactorial control.

The probabilities for linkage between hindwing ventral yellow bar, hindwing white margin, white head color, costal spot, forewing yellow line and forewing white fleck have been calculated from the 2 × 2 tables constructed by considering the two phenotypes "west Ecuador" and

TABLE XIII.

| Brood | Parentage | F/W Yellow Line | | H/W Yellow Bar | | | H/W White Margin | | | Costal Spot | | Head Color | | | F/W Fleck | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | *cy* | $F_1$ & *fl* | *cy* | $F_1$ | *fl* | *cy* | $F_1$ | *fl* | *cy* | $F_1$ & *fl* | *cy* | $F_1$ | *fl* | *cy* | $F_1$ & *fl* | Total |
| M4 | (*cytherus* × *flagrans*) ♂ × (*cytherus* × *flagrans*) ♀ | 0 | 13 | 0 | 8 | 5 | 0 | 5 | 8 | 1 | 12 | 3 | 6 | 4 | 0 | 13 | 13 |
| M8 | Replicate of M4 | 3 | 13 | 4 | 9 | 3 | 4 | 9 | 3 | 3 | 13 | 6 | 5 | 5 | 3 | 13 | 16 |
| $F_1X$ | Replicate of M4 | 3 | 3 | 3 | 1 | 2 | 2 | 2 | 2 | 1 | 5 | 2 | 2 | 2 | 3 | 3 | 6 |
| | Total | 6 | 29 | 7 | 18 | 10 | 6 | 16 | 13 | 5 | 30 | 11 | 13 | 11 | 6 | 29 | 35 |

"not west Ecuador." This has been done to reduce errors caused by misclassification of phenotypes and the results are presented in Table XIV together with the maximum likelihood estimates for the crossover values. From the table it is clear that the genes controlling bar, margin, forewing line and fleck, lie between those controlling costal spot on the one hand and head color on the other. However, because of the large standard errors involved in the estimates and the disturbing effect of a small amount of misclassification of the phenotypes, the order of the genes, bar, margin, forewing stripe and fleck cannot be determined from the data with certainty. However, the most probable order on the chromosome is costal spot, white margin, yellow bar, fleck, forewing line, head color, with the genes controlling margin, bar, fleck and forewing line showing a very close linkage one with the other.

### Tenth Experiment: (F$_1$ *cytherus* × *flagrans*) × *plesseni*

For reasons not understood the stocks of *plesseni* from eastern Ecuador never became established. Eggs were laid and larvae hatched but no adults were produced. However, though at the time it was considered a joke, a mating was effected between a *cytherus* × *flagrans* F$_1$ female and a wild double-banded *plesseni*. The five progeny are classified in Table XV.

*Expansion*—The forewing bands of all the progeny were short and more or less divided, as in the *erato* (*notabilis* × *adanus*) crosses. The progeny all had a costal spot, a preponderance of yellow on the head, and one specimen had both "shadow" ventral yellow bar and "shadow" hindwing white margin. The other specimens were as *flagrans* with neither. The data suggest that the

TABLE XIV.

| Costal Spot | H/W White Margin | H/W Yellow Bar | F/W Fleck | F/W Yellow Line | Head Color |
|---|---|---|---|---|---|
| Costal Spot | 19.1 | 21.5 | 18.8 | 28.6 | 38.0 |
| p | .029 | .044 | .026 | .195 | .082 |
| | H/W White Margin | 6.3 | 7.4 | 7.4 | 38.9 |
| | p | $10^{-6} \times 5.2$ | $10^{-4} \times 1.26$ | $10^{-4} \times 1.26$ | .295 |
| | | H/W Yellow Bar | 3.2 | 3.2 | 37.4 |
| | | p | $10^{-6} \times 4.31$ | $10^{-6} \times 4.31$ | .021 |
| | | | F/W Fleck | 6.7 | 22.7 |
| | | | p | $10^{-4} \times 1.07$ | .007 |
| | | | | F/W Yellow Line | 33.0 |
| | | | | p | .063 |

TABLE XV.

| Brood | Parentage | Phenotypic Characters of Forewing Band of Progeny | | | | |
|---|---|---|---|---|---|---|
| | | Semidivided | | Divided | | Total |
| | | Round | Truncate | Round | Truncate | |
| SF$_1$ | F$_1$ (*cytherus* × *flagrans*) ♀<br>×<br>*plesseni* ♂ | 1 | 3 | 0 | 1 | 5 |

inheritance of red, division of band, and shape of tip, is in *plesseni* similar to that in the sympatric *erato notabilis*. The Z-band character which is peculiar to *melpomene*, appeared in one of the progeny and was probably carried in *plesseni* for it has not appeared in any *cytherus* × *flagrans* crosses.

## V. Discussion

In the preliminary morphological studies on *Heliconius*, which were reported in Emsley, 1963, it was deduced that *melpomene* is a more primitive species than *erato*, and further unpublished work on a revision of the genus supports this view. The description of the wild populations of *melpomene* shows that there is an incomplete circular cline commencing in western Ecuador, which passes around the spurs of northern Colombia and the highlands of British Guiana to the Amazon basin, and which terminates along the eastern slopes of the Andes and in southern and eastern Brazil. From any point in this area there are clines of minor variation which associate almost all the forms of *Heliconius* placed in the Melpomeneformes by both Stichel & Riffarth (1900) and Neustetter (1929). Direct confirmation of this widespread conspecificity has been obtained by the laboratory breeding of the geographically distant forms *cytherus*, *flagrans* and *plesseni* from western Ecuador, Trinidad and eastern Ecuador respectively. The only forms over which doubt exists are *heurippus*, *timaretus*, *besckei* and *tumatumari*.

*Heliconius melpomene heurippus* is a very constant form, confined to the valleys of the Guatiquía river above Villavicencio in eastern Colombia, and with which there are no known graded intermediates. There are, however, a few museum specimens from neighboring localities (*wernickei*, *emilius* and *rubellius*) which exhibit discrete intermediate characters between *heurippus* and the neighboring *melpomene rosinus*, and *Heliconius cydno*. These are considered to be wild hybrids, for the large red and yellow forewing band of *heurippus* could act as a courtship releaser for both the red-banded *rosinus* and the yellow-banded *cydno* (see Crane, 1955). The small differences that can be detected in the genitalia of *cydno*, *heurippus* and *rosinus* are not considered of importance for it has already been established (Emsley, *loc. cit.*) that there is no "lock and key" mechanism in *Heliconius* coition. Closely related species may or may not have identical genital valves, just as the genital valves may vary to a small degree over the range of a widely distributed continental species, or in isolated communities. The lack of graded intermediates between *heurippus* and the other morphs of *melpomene* can be explained by the altitudinal barriers presented by the head of the Guataquía valley and the uninhabited, inaccessible and uncollected nature of the territory to the southeast where intermediates could be expected to occur. Though the isolation of *heurippus* is comparable with that of the other forms of *melpomene* in the valleys of the eastern Andes, it is possible that it has become specifically distinct, but the structure and the coincident locality data of *emilius*, *rubellius* and *wernickei* leave no doubt that fertilization with *cydno* and *rosinus* has been effected. The detailed evidence for this will be presented in the revision of the genus.

It is now well established that the Amazon basin is occupied by yellow-banded *melpomene* which also exhibit dennis and ray. Along the slopes of the Andes, at about 850 meters at the equator, at 250 meters at 15° South and at pro rata altitudes in between, the yellow band gives way to one which is red or nearly all red and dennis-ray is lost. Only in the valleys of the Santiago and perhaps the Napo rivers is the yellow retained, then in a minimal condition. The occurrence of the yellow-banded dennis-rayed *timaretus* in the valley of the Pastaza and other rivers is inconsistent with this over-all generalization and is the only known exception. Specimens exhibiting variously graded intermediate characters are known from eastern Ecuador and Peru *(erebius, pluto)* which confirm the relatively wide distribution of the *timaretus* complex and associate it with undoubted members of *melpomene*. The scarcity of reliable and detailed locality data severely handicaps the interpretation of the situation, but as all the altitudes recorded are above those known for the non dennis-ray red-banded forms, it is most likely that *timaretus* is a highland form which maintains continuity around the spurs which sucessfully isolate the characteristic valley forms. There are no morphological grounds for regarding *timaretus* as a distinct species and there are no known sympatric species of *erato*.

In southern and southeastern Brazil the distribution of *besckei*, as judged by museum data, is discontinuous with that of *melpomene nannus*, so there is also a discontinuity in the distribution of the hindwing red arcs which are peculiar to *besckei*. The genital valves of *besckei* are a little different from those of *nannus* but the territory in the neighborhood of the Paraná river, which appears to separate them, is most inadequately collected. The two forms are so similar in morphological and wing-pattern detail that pending further data *besckei* will be considered conspecific with *melpomene*.

The status of *tumatumari* and *bari* are in doubt because they differ from other *melpomene* forms by the addition of a sub-apical forewing band and irregularities in the minor characters. They are known by very few specimens from the Guianas and are in other respects typically *melpomene*.

There can be no doubt now that all the forms of *Heliconius* listed by Neustetter under the Eratoformes are one species conspecific with *erato*. That *cyrbius, notabilis* and *adanus* from western, eastern Ecuador and Trinidad respectively, are conspecific has been demonstrated by breeding, and in the wild they are associated by being parts of an incomplete circular cline directly comparable with that pertaining in *melpomene*. All the known forms can be interconnected by graded series of intermediates though the rate of change is greater up the slopes of the eastern Andes than elsewhere.

The high degree of coincidence in the appearance and distribution of comparable wing characters in *erato* and *melpomene* is remarkable, for not only do the conspicuous components like wing band, yellow bar, iridescence and hindwing white margin match up in sympatric pairs, but the less conspicuous minor characters like head color, forewing yellow line, reduction of basal spots and loss of costal spot coincide too. With such a detailed and widespread similarity in color and pattern the possibility of this situation having arisen by chance alone can be disregarded, and the conception of mimicry must be accepted.

In the earlier paper on the Heliconiinae (Emsley, *loc. cit.*) it was shown that upon an examination of the species available in Trinidad it seemed likely that the genus *Heliconius* could be divided into three main stems. The most primitive group contained most of the members of the old genus *Eueides*, from which had arisen the *numatus, doris, wallacei, melpomene* association, and from which again had arisen the more advanced group containing *erato, ricini* and *sarae*. As *melpomene* and *erato* had so very many superficial characters in common it was considered that *erato* must have separated from *melpomene* and then given rise to the ancestor of the other species in its group. It is now possible to bring more detailed data to bear on the validity of the resemblances between *erato* and *melpomene* as a result of the recently completed breeding program.

Blue iridescence has been shown to be most probably under multifactorial control in both *melpomene* and *erato*. Considering the wide occurrence of iridescence in nearly related species of *Heliconius*, it may well be an ancestral character.

The shape of the forewing band of both species has been shown to be under very similar multifactorial control in western Ecuador and Trinidad. Turner & Crane (1962), in crosses with Guianese stock, identified a major locus for width of band in both *melpomene* and *erato*, and from the evidence in this paper it seems that there is a major factor or factors for shortness and division of band in both species in eastern Ecuador. The performance of tip control in eastern Ecuador also seems similar. The narrow-banded anomalies discovered by Sheppard (1963) are being re-examined by Turner, for it seems likely that there are multiple allelomorphs available at some loci. In both *melpomene* and *erato* red is dominant to both yellow and white. Though red and yellow occur in both species, yellow is the only forewing band color known to occur in the remainder of the genus, with the exception of *hermathenae*, and the monomorphic red-bands are all quite unlike any other band shapes in the genus. It seems more likely that yellow is the ancestral color, and red has been acquired independently in each species, than that red had been acquired by their mutual ancestor and independently they have reverted to yellow. If *tumatumari* is a good *melpomene* it supports this hypothesis, for the double nature of the yellow forewing band is very similar to that occurring in many of the other yellow-banded species of *Heliconius*.

Hindwing white margin is in both species controlled by a single pair of allelomorphs with its presence semirecessive to its absence. White margin is a feature of wide occurrence in near-relatives of both *melpomene* and *erato* which could have been present in the common ancestor.

Hindwing ventral yellow bar is again controlled by a single pair of allelomorphs with its presence semirecessive to its absence. There are no data on dorsal yellow bar, but from museum specimens there do appear minor differences in its genetic behavior, particularly between northern and southern *erato*. This character is of wide occurrence in the sylvaniforms, which are very close to *melpomene*, and in other closely related species. It does not occur in near-relatives of *erato*. There is evidence of close linkage between white margin and ventral yellow bar in both species ($p<0.001$). In *erato* the maximum likelihood estimate for the crossover value is 14.4% ± 1.22% whereas in *melpomene* it is 6.5% ± 2.8%. The figure for *erato* may well be lower in the absence of errors in scoring. This close agreement in linkage, taken together with the similarities in heterozygous expression and the presence of ventral yellow bar in all localities in both species where dorsal yellow bar occurs, suggests most strongly that it is an ancestral character.

Head color and costal spot in both *melpomene* and *erato* each appears to be under the control of a single pair of allelomorphs without dominance.

Forewing yellow line was not represented in the *erato* material studied and forewing white fleck does not occur in *erato,* but in *melpomene* both these characters were controlled by a single pair of allelomorphs with the presence of the character recessive to its absence.

In *erato* the data are imperfect and linkage can only be demonstrated between hindwing ventral yellow bar and white margin, though the data do not exclude the possibility of linkage between other studied characters. In *melpomene* there is evidence for linkage between all the wing pattern components with the exception of color, upon which there were no data. Though the data have not been presented, there is in *melpomene* a suggestion of linkage between some of the polygenes for band shape and yellow bar.

Accepting mimicry between these two species as a fact, the chance of two distantly related species having such a similar genetical constitution seems small, and the alternative is to concede that they are systematically closely related.

If one can accept that the similarities in *erato* and *melpomene* are the result of parallelism rather than convergence, those features which have a similar genetic performance in the two species were probably common to the mutual ancestor, whereas those that are different have had an independent origin or were represented in a polymorphic ancestral population. The data discussed above suggest that the mutual ancestor of *melpomene* and *erato* was a *Heliconius* with a blue iridescent ground color, yellow forewing band, a hindwing ventral yellow bar, a white margin to the hindwing and perhaps with a forewing yellow line and a dorsal yellow bar on the hindwing. The prevalence of basal red spots in the near relatives suggests that these were represented in a pattern not dissimilar to that of modern *melpomene.*

The substantial difference between the ray pattern in *melpomene* and *erato* could be explained if one postulates that the ancestral species was allopatrically polymorphic for this character, as *Heliconius doris* is at present. In *doris* there are two distinct ray patterns, a northern form which is almost exactly like the ray pattern of *melpomene timaretus* but with the bar of dennis incorporated proximally, and a southern pattern which is hardly distinguishable from that of *erato,* and six other species of *Heliconius.* In this theoretical discussion it is suggested that *melpomene* was derived from a population of the ancestral species which possessed the characters previously outlined and the *melpomene*-type ray; *erato* on the other hand evolved in isolation from another population of the ancestral species in which the *erato*-type ray was additional to the common characters. The occurrence of differences in the phenotypic expression of dennis presents a difficulty that can only be overcome by postulating a specific modification in the case of *melpomene,* for dennis as it occurs in *erato* is of wide occurrence in *Heliconius.* Some support is given to this hypothesis by the comparable linkage of dennis, ray and a band character in both species (Turner & Crane, 1962; Sheppard, 1963).

There are so many unknowns in the postulation of an evolutionary history for *melpomene* and *erato* that many biologists will feel it should not be attempted until more data are available, but the opportunities for the accumulation of more data are so few that it is likely that many years will elapse before really substantial evidence can be presented. The author feels, however, that if the hypothesis presented below provokes discussion among interested readers, new ideas may appear which would not otherwise have been considered. If this is so, then it is justified.

On the premise that the mutual ancestor was of the pattern described above, and the two characteristic ray morphs were allopatric and subsequently isolated from each other, then the two populations would have evolved along independent lines.

The author's knowledge of the geological and climatic history of the South American continent is insufficient to enter into discussion of where such geographical isolation took place or even how long ago. It is certain that the glacial periods have had a profound effect on the distribution of the Neotropical fauna, and one must not think of South America as having remained as is now during the evolution of even the geographical races of *melpomene* and *erato.*

It is suggested that the northern (?) population, which possessed the *melpomene*-type ray, evolved a red and yellow forewing band like that known in *heurippus* now. Such a red and yellow color combination would not have necessitated co-adaptation of the courtship releaser mechanism. The evolution of dominance of red together with the evolution of red as a courtship releaser would present a situation similar to that which we believe currently pertains in the peripheral region of South America. One must assume that the factors that have prevented *melpomene* becoming an all-red-banded species were the same then as they are today. The author's experience on the eastern slopes of the Ecuadorian Andes may be important here.

Puyo is located at an altitude of just under 1,000 meters on a tributary of the River Pastaza, and the only morphs of *melpomene* and *erato* that occur there are black with a double red and white forewing band. They confine themselves principally to streams, paths and glades in the interior of the forest and only occasionally do either of them fly beyond forest margins. Their light and dark pattern and erratic flight make their position very hard to estimate when trying to catch them, even though they do not fly very powerfully. One cannot help but notice the almost total absence of "tiger"-patterned butterflies. There are very few danaids, and those there are have a single broad orange forewing band, with no suggestion of yellow and black, and they confine themselves to the interior of the forest. There are few *Heliconius isabellus* or near relatives, and very few Sylvaniformes and those that are present are patterned like the danaids with which they fly.

No more than 40 km. east, and after a descent of only 100 meters, the scene changes abruptly and spectacularly. "Tiger"-patterned Sylvaniformes, *isabellus,* danaids and ithomiines abound on the vergeside flowers, and all the *melpomene* and *erato* seen are with a double-yellow or white forewing band and dennis-ray. They fly in exposed positions and with a much more purposeful manner than those from the higher altitudes. The visual effect of a "tiger"-patterned danaid and a yellow-banded dennis-rayed *Heliconius* is, to human eyes, very similar. From the body there are in successive order on each side, a broad orange-red band, a yellow band and a black tip. The author had considerable difficulty in distinguishing them in flight.

This experience was so impressive that it may well be an effect which has governed the distribution of yellow band in *erato* and *melpomene* for a considerable period of their history. One would infer that where danaids and the less diaphanous ithomiines are the ecologically dominant groups, selection for yellow-band and dennis-ray is stronger than any other force. Where the populations of these proved distasteful groups are low, as in Trinidad and above 900 meters in eastern Ecuador, selection for yellow band and dennis-ray is low and courtship selection for red, together with dominance of red over yellow, maintains an all-red population. In intermediate areas like the Guianas, southern Colombia and Bolivia where the two types of pattern meet, there is a region of polymorphic hybridization which is kept in a state of dynamic equilibrium by the opposing forces on either side of the zone.

If the area in the Amazon basin currently occupied by yellow-band and dennis-ray was in the past a little smaller than it is now, then the red-banded forms could have occupied the foothills of the Andes quite broadly, and with an increase in the range of the yellow band dennis-ray, presumably on account of the increase in the range of the danaids, the red-banded non-dennis-ray forms would have been cut off in the river valleys of the eastern Andes, which is the situation in which we find them today.

The most obvious deficiency in our knowledge in this hypothesis is the quantitative estimate of danaid and other model populations in the region inhabited by *erato* and *melpomene.* This could be obtained by statistically acceptable sampling in a small number of carefully chosen localities on the boundaries of the two zones.

Prior to the segregation of the yellow band dennis-ray and red band non-dennis-ray types, one must assume that the *erato*-rayed population, isolated in the south, rejoined its parent population after specific barriers had become erected.

During the evolution of red forewing band in *melpomene* one must postulate an analagous mutation in *erato,* and also assume the evolution of courtship selection for red. The behavior of red and yellow in combination in *melpomene* and *erato* supports this suggestion, for in the northern part of their range all the red and yellow combinations known in *melpomene* are of the *heurippus* type of interface, whereas the only known type of interface in *erato* is one in which the two colors intermingle over a large area. It is worth noting here that the *heurippus*-type interface also occurs in *timaretus,* which also has the most *doris*-like ray known in *melpomene.* It is the only *melpomene* known to occur in the absence of *erato,* and should perhaps be considered a relic.

Once *erato* had evolved a red forewing band it would have been under the same type of selection forces as *melpomene,* and having a similar basic appearance and genetic constitution, it has maintained a step by step mimetic relationship.

There is one further complexity. There are at present no records of *melpomene* from the east coast of Brazil. If this distribution is the real situation and is one which has persisted during a substantial part of the evolutionary period under discussion, then it is possible that red-banded non-dennis-ray *erato* extended its range around the coast and the Brazilian highlands into southwestern Brazil where it would have met yellow-banded Amazonian *melpomene* and *erato.* The *erato* would have interbred and the red band would have spread until the polymorphic equilibrium was reached, somewhat as it is now in eastern Bolivia. The *melpomene,* however, would have had only yellow band and been unable to enter a mimetic relationship with *erato* in the red zone without an independent mutation for red band color, the *heurippus* band being confined to the north. The successful mutation of a second form of red band in this southern locality could explain why the red yellow interface of southern *melpomene* are not of the *heurippus* type but with yellow and red scales broadly intermingled over a substantial area.

A minor supporting feature is the peripheral distribution of dorsal yellow bar, and the relic retention of white margin at the western extremity of the range of the species. The ventral red raylets on the ventral surface of the hindwing of southern *erato* may be a relic of a line of dots emanating from the basal spots as also occurs in *sarae.* This feature would not have been in southern *melpomene,* as the hypothesis supposes that *erato* arrived there second, so it is not unexpected to find a new feature matching it in the red arcs of *besckei.*

One of the embarrassing aspects of this mimetic situation is the degree of detail in the similarities between the two species. Not only are the general proportions, locations and color of the patterns similar, but the shape of the bands corresponds in detail and the variations of even small characters like costal spot are comparable. The evidence from avian predators of *Heliconius* (Brower, Brower & Collins, 1963) does not suggest that they can appreciate detail of this magnitude, at least not under experimental conditions where one would expect them to have more opportunity for careful scrutiny than in the wild. In view of the close likeness between the genetic constitution of the two species, it seems likely that many of the detailed resemblances are coincidental. The selection for a major pattern-component, whether for the simulation of each other or of a third party, would effect similar changes in the genotype of both species. The genetic units which control the composition of the color-pattern can only respond to a given situation in a basically similar way. It has also to be remembered that the eggs, larvae and pupae all have the same genes, so a character of selective advantage in one stage may produce a neutral but visible effect in another, etc.

The question of whether *erato* and *melpomene* are Batesian or Müllerian mimics has been substantially answered by the data obtained by Brower, Brower & Collins (*loc. cit.*) who found that though both can be classed as unpalatable, *melpomene* was more frequently rejected than *erato.* Whether the relationship has always been Müllerian is a question that cannot be answered, but it is easier to believe that it has than that it has not. If the ancestor was already distasteful before the speciation in which we are interested took place, then the relationship has undoubtedly always been Müllerian. If, however, the common ancestor was palatable, and say *melpomene* was the first to acquire distastefulness, it is difficult to understand how *erato* could have acquired it except by a similar one-step change. Rothschild's view (1963) on how Müllerian mimicry can evolve gradually from a Batesian relationship is interesting. Her view, in essence, is that while the imperfect mimic in a Batesian relationship is under strong selection for good resemblance, once an adequate degree of similarity has been obtained, though the likeness should improve, there will be additional selection for distastefulness. However, unless the insect survives the attack, and is reproductively viable, selection on palatability alone cannot operate. The predator must learn to associate its experience with a visual image which it can remember, so it is not the attacked insect that escapes but another similar one. Unless there is a visually perceptible character in association with unpalatability, though the population as a whole may benefit from the predator's experience, there is no selective advantage gained by the unpalatable members only.

Hitherto, birds have been the only class of predator considered, but the number of eyewitness accounts of birds attacking *Heliconius* is very small, though collectors' fastidiousness will have probably excluded such attacked insects from their collections. In Colombia several terrestrial burrows were found in the forest, at the entrance of which were many *Heliconius* remains. The occupants of the burrows are unknown. Lizards have good color vision and members of the genus *Ameiva* have been an occasional nuisance in the mating cages, for once they have gained entrance, they climb the wire-netting and lie in wait by the floral food supply, and snap at butterflies as they settle.

## VI. Conclusions

1. The Eratoformes and the Melpomeneformes, as catalogued by Neustetter (1929), are each a single species, *Heliconius erato* and *melpomene* respectively, which exhibit pronounced geographical variation.

2. The two species are grossly sympatric and maintain a close mimetic relationship over their whole range.

3. The two species are held to be systematically closely related on account of the very similar genetic performance of the characters studied. Experiments between material from western Ecuador and Trinidad have shown that in both

species the shape of the forewing band and the intensity of the iridescence are under multifactorial control. The inheritance of hindwing ventral yellow bar, hindwing white margin, head color and the presence of costal spot is in both species controlled by a single pair of allelomorphs with similar dominance and similar heterozygotic expression. There is evidence of close linkage between ventral yellow bar and hindwing white margin in both species. In *melpomene,* all the pattern components were shown to be linked, but though no such linkage was demonstrated in *erato,* the possibility of such linkage cannot be denied. Though no comparison could be made, the forewing yellow line and forewing fleck of *H. melpomene* in western Ecuador also appear to be under the control of a single pair of allelomorphs.

Experiments between material from eastern Ecuador and Trinidad show that in *erato* the outer band tip-shape is controlled by a single pair of allelomorphs and there is a major factor, or pair of very closely linked factors, of considerable penetrance controlling shortness and division of the forewing band. Though the evidence is inconclusive, it is likely that the situation in *melpomene* is similar.

4. From the distributional data, it is shown that the yellow-banded dennis-rayed non-yellow-barred forms of both species in the Amazon basin are surrounded by red-banded yellow-barred non-dennis-rayed forms. The view is held that the stability of the Amazonian forms is maintained by strong selection for resemblance to danaids and other distasteful butterflies whose wing pattern from apex to base forms the series black-yellow-orange.

5. It is suggested that the stability of the peripheral red-banded non-dennis-rayed populations is maintained by the importance of red as a courtship releaser, the dominance of red over yellow and white and the weak selection for resemblance to the less abundant danaid-type models.

6. The opinion is held that the polymorphism in the Guianas, east-central Colombia, the eastern slopes of the Andes and in Bolivia, is a dynamic equilibrium brought about by the opposing influences mentioned in 4 and 5 above.

7. The exceptionally close similarity between sympatric forms of *melpomene* and *erato* is deemed to be due primarily to their close systematic relationship. Their genetic constitution is so similar that having been subjected to common selective forces since becoming specifically distinct, they have been able to respond to selection only in a very similar way. It is thought that in the Amazon basin there is a triangular mimetic relationship between the strongly distasteful models at one corner and *erato* and *melpomene* at the other two, so each has effected a compromise in attaining the pattern exhibited by the other two competitors. Beyond the dominating influence of the Amazonian danaids there is only a dual Müllerian relationship between *erato* and *melpomene.*

## VII. Summary

1. The color-pattern components of the wings of *Heliconius erato* and *H. melpomene* are described and their distribution recorded.

2. It is shown that both the major and minor color-pattern components are comparable and similar components occur only sympatrically in the two species.

3. By laboratory breeding it was established that *H. erato cyrbius, adanus* and *notabilis* are conspecific, and *H. melpomene cytherus, flagrans* and *plesseni* are also conspecific. From the data and a survey of museum material, it is inferred that all named forms catalogued by Neustetter (1929) in the Eratoformes and Melpomeneformes are members of the two species *erato* and *melpomene* respectively.

4. The genetical data presented indicates a close similarity in the performance of the genes controlling forewing band, ventral yellow bar, hindwing white margin, head color and forewing costal spot in populations of both species from western Ecuador and Trinidad. These similarities in genetical constitution suggest that the two species are systematically closely related.

5. The evolution of the color patterns in the two species is discussed with particular reference to mimicry.

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APPENDIX: Brood-rearing Data, Showing the High Incidence of Mortality Which Is Almost Entirely Attributed to Virus Disease

| Brood | Parentage | Duration of Oviposition in Days | Numbers of Eggs Laid | Numbers of Larvae | Numbers of Pupae | Numbers of Adults |
|---|---|---|---|---|---|---|
| | Original *cyrbius* females | 21 | 19 | 19 | 10 | 9 |
| | Original *notabilis* females | 14 | 20 | 20 | 9 | 5 |
| | *cyrbius* × *cyrbius* (stock) | | 60 | 51 | 19 | 17 |
| | *notabilis* × *notabilis* (stock) | | 201 | 176 | 31 | 16 |
| | *adanus* × *adanus* (stock) | | 65 | 64 | 15 | 11 |
| Pb1 | *cyrbius* × *adanus* | 108 | 103 | 94 | 28 | 24 |
| Pb2 | *cyrbius* × *adanus* | 133 | 117 | 109 | 27 | 26 |
| Pa1 | *cyrbius* × *adanus* | 138 | 235 | 211 | 52 | 40 |
| C17 | *cyrbius* × *adanus* | 64 | 84 | 61 | 30 | 28 |
| C12 | (*cyrbius* × *adanus*) $F_2$ | 16 | 19 | 19 | 8 | 8 |
| C4 | (*cyrbius* × *adanus*) $F_2$ | 54 | 60 | 58 | 23 | 18 |
| C3B | (*cyrbius* × *adanus*) $F_2$ | 53 | 22 | 6 | 0 | 0 |
| C2A | (*cyrbius* × *adanus*) $F_2$ | 8 | 18 | 16 | 0 | 0 |
| C19 | (*cyrbius* × *adanus*) $F_2$ | 6 | 3 | 3 | 0 | 0 |
| $F_1$X2 | (*cyrbius* × *adanus*) $F_2$ | 33 | 37 | 30 | 0 | 0 |
| C2 | (*cyrbius* × *adanus*) × *adanus* | 20 | 36 | 25 | 1 | 1 |
| C5A | (*cyrbius* × *adanus*) × *adanus* | 96 | 104 | 98 | 25 | 20 |
| BXWE | (*cyrbius* × *adanus*) × *cyrbius* | 52 | 86 | 63 | 0 | 0 |
| C13 | (*cyrbius* × *adanus*) × *cyrbius* | 142 | 156 | 148 | 29 | 17 |
| C14A | (*cyrbius* × *adanus*) × *cyrbius* | 101 | 98 | 70 | 12 | 5 |
| C18 | *notabilis* × *adanus* | 61 | 71 | 64 | 12 | 9 |
| C5B | *notabilis* × *adanus* | 31 | 44 | 33 | 2 | 1 |
| C14B | *notabilis* × *adanus* | 24 | 25 | 8 | 6 | 3 |
| C11 | *notabilis* × *adanus* | 5 | 6 | 6 | 1 | 1 |
| C15 | (*notabilis* × *adanus*) $F_2$ | 21 | 23 | 10 | 9 | 1 |
| C7 | (*notabilis* × *adanus*) × *adanus* | 96 | 84 | 72 | 54 | 47 |
| C6 | (*notabilis* × *adanus*) × *adanus* | 30 | 50 | 48 | 10 | 8 |
| C16 | (*notabilis* × *adanus*) × *adanus* | 53 | 65 | 60 | 38 | 27 |
| C19 | (*notabilis* × *adanus*) × *notabilis* | 24 | 34 | 20 | 1 | 1 |
| Ma | *cytherus* × *flagrans* | 99 | 248 | 175 | 52 | 44 |
| M4 | (*cytherus* × *flagrans*) $F_2$ | 74 | 142 | 83 | 19 | 13 |
| M6 | (*cytherus* × *flagrans*) $F_2$ | 6 | 4 | 0 | 0 | 0 |
| M8 | (*cytherus* × *flagrans*) $F_2$ | 25 | 96 | 50 | 20 | 16 |
| $F_1$X | (*cytherus* × *flagrans*) $F_2$ | 41 | 77 | 36 | 8 | 6 |
| TX2 | (*cytherus* × *flagrans*) × *flagrans* | 38 | 40 | 36 | 0 | 0 |
| $F_1$BX | (*cytherus* × *flagrans*) × *flagrans* | 36 | 98 | 87 | 3 | 2 |
| M5 | (*cytherus* × *flagrans*) × *cytherus* | 10 | 5 | 3 | 1 | 1 |
| S$F_1$ | (*cytherus* × *flagrans*) × *plesseni* | 21 | 36 | 29 | 6 | 5 |

SUMMARY

| Eggs Laid | Eggs Hatched | Larvae Pupated | Pupae Emerged | % Insects Successfully Reared of Eggs Laid |
|---|---|---|---|---|
| 2691 | 2161 | 561 | 430 | 16.0% |

## EXPLANATION OF THE PLATE

### PLATE I

The color components of the wing patterns of *Heliconius erato* and *melpomene*. Approximately twice natural size.

FIG. 1. Dorsal view of a right forewing illustrating black ground color; double yellow band; dennis; and fully developed forewing yellow line.

FIG. 2. Dorsal view of a right forewing illustrating blue iridescent ground color; short narrow red band as it occurs in *cyrbius;* and yellow basal spot.

FIG. 3. Dorsal view of a right hindwing of a male *melpomene* illustrating bar of dennis; white margin as it occurs in *cytherus;* and black ground color.

FIG. 4. Dorsal view of a right hindwing of a female *erato* illustrating blue iridescent color; dorsal yellow bar; and white margin as it occurs in *cyrbius.*

FIG. 5. Dorsal view of right hindwing of male *erato* illustrating ray on black ground color.

FIG. 6. Dorsal view of right hindwing of female *melpomene* illustrating non-dennis ray on black ground color.

FIG. 7. Ventral view of right hindwing of *erato* illustrating brown ground color; yellow bar; yellow costal streak; red basal spots; apical cream rectangles; and raylets.

FIG. 8. Ventral view of right hindwing of *melpomene* illustrating brown ground color; yellow bar; yellow costal streak; red basal spots; and submarginal red arcs with their apical cream rectangles.